MID-DEVONIAN CHONDRICHTHYAN SCALES FROM THE BROKEN RIVER, NORTH QUEENSLAND, AUSTRALIA

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Chondrichthyan scales from mid Emsian to earliest Frasnian of the Dosey-Craigie Platform, Broken River region, northern Queensland include three new form genera, *Gondwanalepis, Notiolepis,* and *Aussilepis,* each represented by new species: *G. grossi, N. dienemos,* and *A. lukaso.* Also present are *Cladolepis* sp. cf. *C. gunnelli,* and scales tentatively referred to *Ohiolepis* sp. The diverse fauna includes acanthodian, crossopterygian, palaeoniscoid and thelodont scales; placoderm platelets; onychodontid, palaeoniscoid and indeterminate chondrichthyan teeth; a dipnoan toothplate; and bone fragments of various affinities.□ *Chondrichthyan, Devonian, Eifelian, Givetian, Queensland.*

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The Broken River Group of north Queensland, covering approximately 320km^2, is dated late Early to earliest Late Devonian; the biochronology of the area is described by Mawson & Talent (1989). The Dosey-Craigie Platform, from where the new material was collected, is the southernmost of two shallow marine mixed carbonate and siliciclastic shelf sequences in the area (Fig. 1).

Numerous sections of the Dosey-Craigie Platform have been sampled over recent years, leached with acetic acid, and examined for conodonts by the Mawson-Talent team of the Macquarie University Centre for Ecostratigraphy and Palaeobiology (MUCEP); abundant microvertebrate remains have been recovered from these residues. A diverse fauna has been recognised: acanthodian, chondrichthyan, crossopterygian, palaeoniscoid and thelodont scales; placoderm platelets; onychodontid, palaeoniscoid and indeterminate chondrichthyan teeth; a dipnoan toothplate; and bone fragments of various affinities. A description of the chondrichthyan scales is given here; descriptions of other taxonomic groups are in progress. Conodont determinations (Mawson & Talent, 1989) for the mid-Emsian to late-Givetian interval give precise ages for horizons containing the scales.

Fish remains from the Dosey-Craigie Platform occur in several stratigraphic units: the Papilio Formation (shales with subordinate siltstones and nodular limestones - Givetian), the Spanner Limestone Member of the Papilio Formation (bioclastic, well-bedded and frequently nodular limestone - *varcus* Conodont Zone), the Stanley Limestone Member of the Mytton Formation (bioclastic limestone - late Givetian to earliest Frasnian, late *hermanni-cristatus* to early *asymmetricus* conodont zones), the Lomandra Limestone (mostly calcarenites and calcisiltites - Emsian-Eifelian, *serotinus* to *costatus* conodont zones), the Bracteata Formation (mudstones and lithofeldspathic sandstones, late Emsian *serotinus-patulus* conodont zones), and the Dosey Limestone (calcarenties and calsiltites, late Eifelian-early Givetian, *kockelianus-ensensis* conodont zones). Mawson & Talent (1989, fig. 2) summarised the stratigraphic relationships between these units. The Papilio Formation and associated Spanner Limestone Member contain by far the most abundant fish microfossils. These sediments were laid down in deeper water than, for example, the Lomandra and Dosey Limestones, formed under shallow water conditions or possibly sometimes exposed (Mawson & Talent, 1989).

The chondrichthyan scales described herein occur in thirteen sections from the Dosey-Craigie Platform succession - SD15, SD128, SD130, SD131, SD146, SD164, SD170, SD190, SD192, SD196, SD204, SD210, and SD216 (Fig. 2). Table 1 lists the geographical location of the sections. All the scales occur in horizons dated *kockelianus* to *hermanni-cristatus* conodont zones, with two forms extending into the Frasnian *asymmetricus* Conodont Zone (Fig.3). In addition to possible changes in the fauna through time, this distribution was probably influenced by facies differences (see above). Most taxa have a range spanning all or part of *varcus* Conodont Zone, the age of horizons in the richly fossiliferous Papilio Formation.

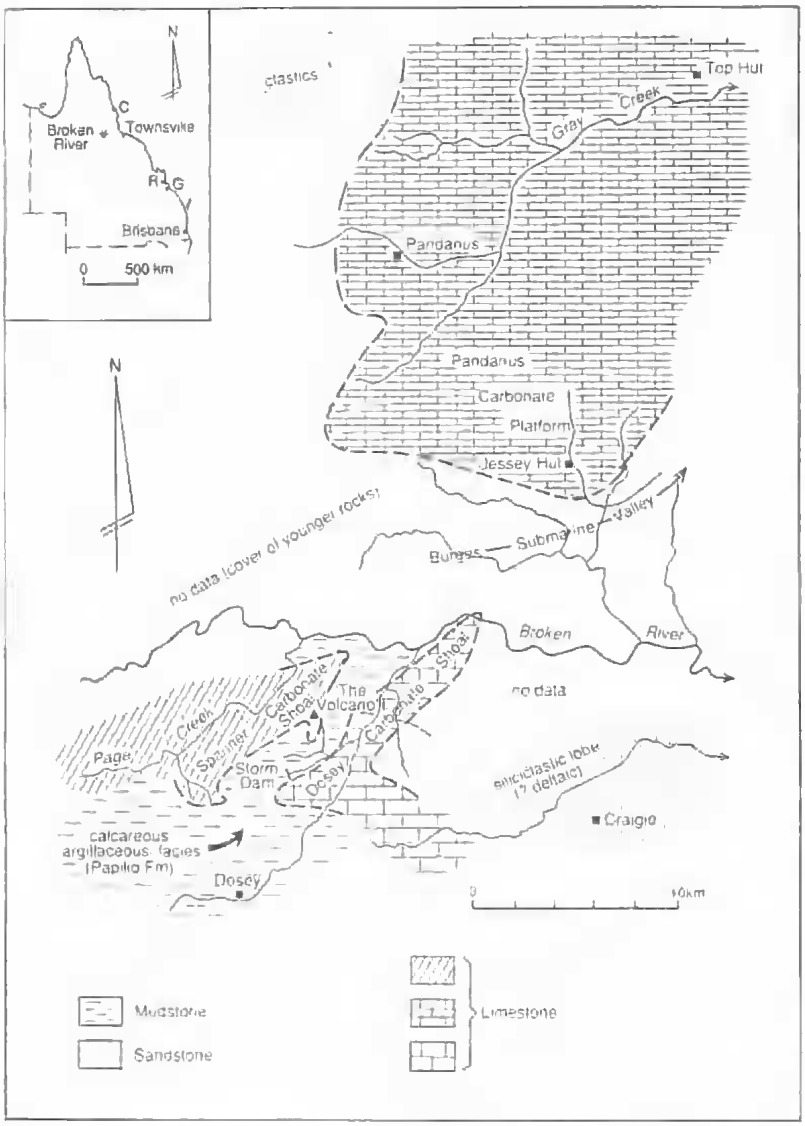


FIG. 1. Palaeogeographic and lithofacies relationships of the Broken River Group during Givetian times (from Mawson and Talent, 1989: fig. 3).

No chondrichthyan scales have been formally described from the Early or Middle Devonian of the Broken River Group, although scales and teeth have been found in acid-leached residues (Turner, 1991; 1993). Turner (1982) described and illustrated shark teeth from the Late Devonian and Early Carboniferous from the northern (Pandanus) platform: *Thrinacodus ferox* Turner, 1982, *Phoebodus* cf. *P. politus* Newberry, 1889, and three species of *Protacrodus*, all dated as "probably Famennian" - and *Stethacanthus thomasi* Turner, 1982 and *Xenacanthus* sp. from the Early Carboniferous. Two new antiarchs, *Wurungulepis denisoni* and *Nawagiaspis wadeae*, were described by Young (1990) from the Broken River Group of the southern (Dosey-Craigie) platform. Turner (1993) reported several forms from the immediate area: an early phoebodont tooth from the Papilio Formation; *Cheiracanthoides comptus* Wells, 1944 scales, onychodontid teeth, palaeoniscoid remains and new shark scales from Fish Hill; turiniids and scales resembling nikoliviids from the Broken River Group; and endemic turiniids, buchanosteid and possibly rhenanid scales, nostolepid scales and platelets and onychodontid teeth from the *pesavis-sulcatus* conodont zones of the underlying Martins Well Limestone.

Remains of chondrichthyans and other groups have been reported from the surrounding region. Turner (1991: fig. 5 i, j) noted and illustrated shark scales and teeth in Middle and Late Devonian limestones from the Broken River area, and reported (Turner, 1993) endemic thelodonts and *Turinia australiensis* Gross, 1971 from Lochkovian horizons of the Broken River Embayment.

Early and Middle Devonian chondrichthyans have been reported in the literature from other areas of Australia and overseas; forms described as chondrichthyan are summarised (Tables 2, 3). It should be noted, however, that the chondrichthyan affinities of some of these forms have subsequently been questioned.

Localities and sections bear the prefix "SD" for Storm Dam (Fig. 2). Specimens are housed in the

palaeontological collections of the Queensland Museum (QMF).

SYSTEMATIC DESCRIPTION

Subclass CHONDRICHTHYES
Infraclass ELASMOBRANCHII

REMARKS

The scales described below are interpreted as chondrichthyan by the presence of neck canal openings and a bony diamond-shaped base, characters considered diagnostic for the group (Turner, 1991). It is further assumed for the present that the taxa described below belong within the Elasmobranchii, because of overall similarity of scale morphology to that of articulated remains known to belong to elasmobranchs, such as *Antarctilamna prisca* Young, 1982.

Gondwanalepis gen. nov.

ETYMOLOGY

From Gondwana, and the Greek 'lepis' = scale.

DIAGNOSIS

Crown subrhombic or rounded subtriangular, bears eight short parallel ridges deeply dissecting the anterior edge. Posteriorly, crown overhangs base a short way. Neck indented at posterior. Base diamond-shaped or subrectangular, flared into a narrow rim around edges, and gently convex, flat, or gently concave. Six to twelve elliptical openings in posterior neck area.

REMARKS

Gondwanalepis is presumed to be a chondrichthyan because the scales have a diamond-shaped, flat or gently convex base, several neck canal openings at the posterior, and low, narrow, con-

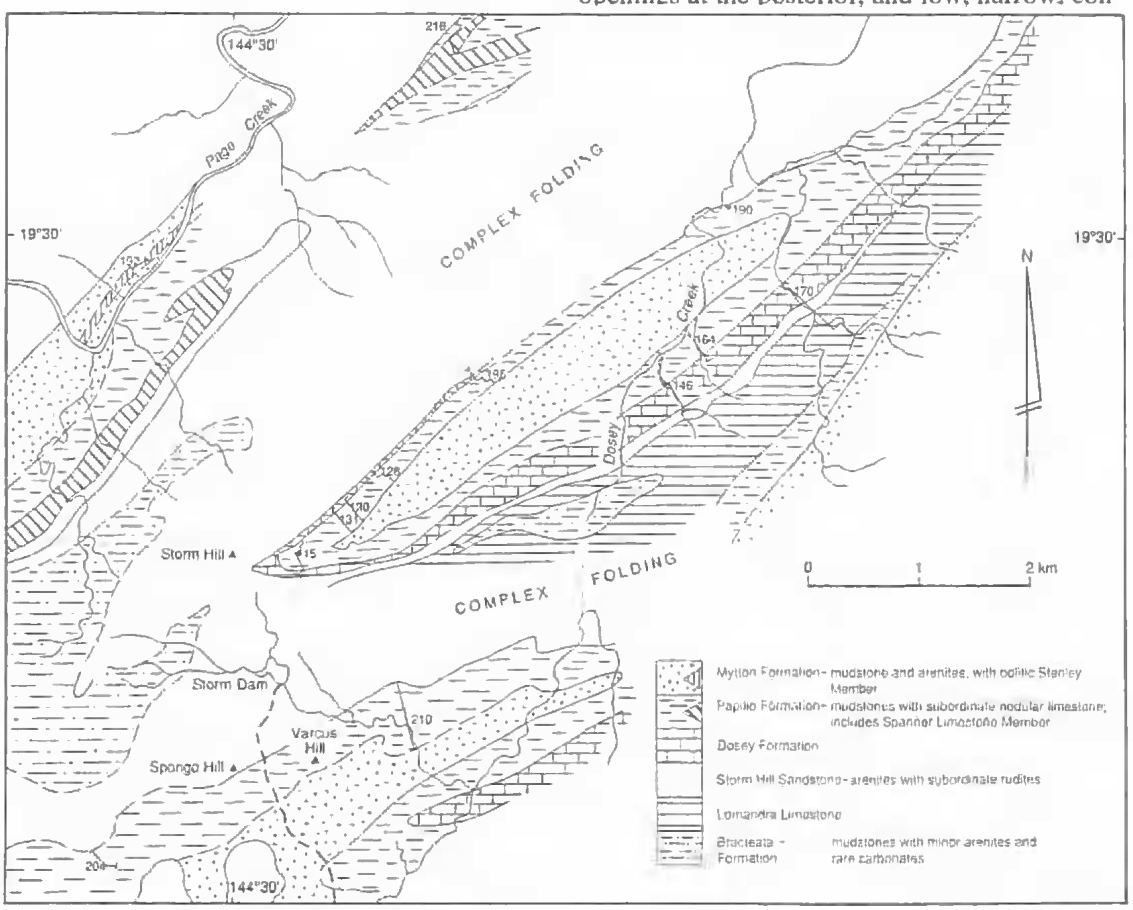


FIG. 2. Broken River Group in the Dosey-Craigie Platform area showing location of stratigraphic sections from which chondrichthyan scales have been recovered (after Mawson & Talent, 1989).

TABLE 1. Geographic localities of the sections mentioned in the text.

Section	Geographic Locality
SD15	(North) - Section commences in small gully tributary to Bracteata Creek at WANDO VALE 558388, across small divide to next gully to SW and extending down it to what is approximately axis of Dosey Syncline. (South) - Continuation of preceding section, traversing across other limb of Dosey Syncline, going down section to contact between Storm Hill Sandstone and Dosey Limestone; section ends at WANDO VALE 558384.
SD128	Section through Papilio Formation, commencing in top of Dosey Limestone in a gully at WANDO VALE 566396, crossing it and terminating over next gully to SE at WANDO VALE 568395, approximately 2 km NNE of Storm Dam.
SD130	Section through Dosey Limestone and Papilio Formation, commencing at WANDO VALE 561392, approximately 1.6 km NNE of Storm Dam.
SD131	Section through Dosey Limestone and Papilio Formation, commencing at WANDO VALE 560391, approximately 1.5 km NNE of Storm Dam.
SD146	Section through Dosey Limestone and Papilio Formation, commencing in Camp Gully at WANDO VALE 596400, approximately 4.3 km NE of Storm Dam and aligned down Camp Gully, crossing Dosey Creek to terminate at high escarpment of Mytton Formation.
SD164	Section through to 7m of Dosey Limestone and through Papilio Formation, commencing in GB Gully at WANDO VALE 601401, approximately 4.8 km NE of Storm Dam and aligned down GB Gully, crossing Dosey Creek to terminate at high escarpment of Mytton Formation.
SD170	Section measured in Lomandra Creek, through Bracteata Formation, Lomandra Limestone, Storm Hill Sandstone, Dosey Limestone and basal beds of Papilio Formation, commencing at WANDO VALE 609398, approximately 6.5 km NE of Storm Dam.
SD190	Spot locality in base of Papilio Formation, at WANDO VALE 600420, approximately 300 metres SSW of junction of Dosey and Lomandra Creeks, and approximately 5.7 km NE of Storm Dam.
SD192	Section through Stanley Limestone Member of Mytton Formation, west of Pages Creek to top of ridge, commencing at WANDO VALE 543415, approximately 4 km NNW of Storm Dam.
SD196	Section through Lomandra Limestone, Storm Hill Sandstone and Papilio Formation, commencing at WANDO VALE 574405, approximately 3.2 km NE of Storm Dam.
SD204	Section through Papilio Formation, commencing at head of gully at WANDO VALE 533360, approximately 2.2 km SW of Storm Dam.
SD210	Section through Papilio Formation, commencing at head of gully, tributary to Storm Dam Creek at WANDO VALE 556376, approximately 1 km ESE of Storm Dam.
SD216	Section through Spanner Member of Papilio Formation, commencing at WANDO VALE 546422, approximately 6 km NNE of Storm Dam.

centric ridges around the posterior margin of the crown. Scale morphology is known in at least 18 genera of Early and Middle Devonian chondrichthyans (Tables 2, 3), but the scales described below cannot be readily referred to any of these.

Wells (1944) assigned scales to three new genera - *Cladolepis*, *Ohiolepis*, and *Deirolepis* - and also illustrated scales of genera *Ctenacanthus*, *Cladoselache*, and *Cladodus* (Wells, 1944: figs 6,7; pl. 3, figs 2-21). Scales of *Gondwanalepis* are like none of these. *Cladolepis* scales have a flat, thin crown ornamented by long curved ridges with shorter, overlapping ridges anteriorly; the crown of *Ohiolepis* scales is covered with numerous anteriorly grooved spines (see further discussion below); *Deirolepis* scales have a long neck and thin base; and scales of *Ctenacanthus*, *Cladoselache*, and *Cladodus* all lack the anterior parallel ridges present on the crown of *Gondwanalepis*.

Gondwanalepis scales are unlike those of *Hercynolepis* in their crown ornamentation. The crown of *Hercynolepis* scales is covered with short, backwardly-pointing, slightly overlapping ribs (Gross, 1973: pl.33, figs 13-15), whereas the crown of *Gondwanalepis* has short, parallel, rounded ribs at the anterior. Scales of *Protacrodus*, also discussed by Gross (1973), differ from *Gondwanalepis* in having a low, flat crown, highly convex base, and distinct furrow where the base joins the neck area (Gross, 1973: pl. 32, figs 3-20; pl. 33, figs 1-12).

Scales of *Polymerolepis* were initially considered heterostracan by Karatajüte-Talimaa (Obruchev & Karatajüte-Talimaa, 1967), but are likely to belong to an Early Devonian shark (Turner & Murphy, 1988). Scales illustrated by Obruchev & Karatajüte-Talimaa (1967) and Turner & Murphy (1988) have the crown heavily ornamented from anterior to posterior with many deep ridges, in most specimens parallel, but sometimes radial; this is quite different from the crown ornamentation of *Gondwanalepis*.

From the Emsian *Receptaculites* Limestone, Giffin (1980) figured two scales referred to Karatajüte-Talimaa's thelodont *Skamolepis*.

These are now considered to be scales of a new chondrichthyan (Turner, 1993). The scales bear no resemblance to *Gondwanalepis* scales in either shape or ornamentation.

Ellesmereia, erected by Vieth (1980), has ridges extending from the anterior right to the posterior margin of the crown, in contrast to the short anterior ridges of *Gondwanalepis*, and the neck of *Ellesmereia* is more constricted.

Gondwanalepis differs from scales of *Antarctilamna* Young, 1982 in having ridges only at the anterior of the crown, in being generally thicker in lateral view, and in lacking a constricted neck and concave, cup-shaped base.

Pruemolepis, when erected by Vieth-Schreiner (1983), was placed in the acanthodian order Climatiida. Mader (1986) transferred the genus to the chondrichthyan subclass Elasmobranchii on the basis of histology. However, *Pruemolepis* scales are now thought to be acanthodian branchial scales (Valiukevicius, pers. comm., 1993). *Pruemolepis* scales have a thicker crown, a more constricted neck, and less conspicuous crown ornamentation than do the scales of *Gondwanalepis*.

Gondwanalepis is unlike the genera from China described by Wang (1984): *Gualepis*, *Changolepis*, and *Peilepis*. *Gualepis*, unlike *Gondwanalepis*, is characterised by a constricted neck and a dentate posterior margin. *Gualepis*-like scales have been recovered from the late Early Devonian Cravens Peak Beds of the Georgina Basin (Turner, 1993: fig. 8.4g,h). *Changolepis*, although having a similar lateral view to *Gondwanalepis*, differs by having a strongly convex central rib on the crown forming a long posterior cusp. The crown of *Peilepis* has anterior flutings and is posteriorly bifurcated, and the flat base has a large elliptical pulp opening.

Scales of the genera erected by Mader (1986), *Arauzia*, *Iberolepis* and *Lunalepis*, differ from those of *Gondwanalepis* in their crown ornamentation. The crown of *Arauzia* scales bears one or several thick, stellate, posteriorly-inclined, pointed tubercles. Both *Iberolepis* and *Lunalepis* scales have parallel ridges extending to the posterior margin of the crown. However, the lateral view of one *Lunalepis* scale illustrated by Mader (1986: pl. 4, fig. 9b) is similar to the lateral view of some scales of *Gondwanalepis*.

Gondwanalepis grossi sp.nov.
(Figs 4; 5; 6A-C)

ETYMOLOGY
For Walter Gross (1903-1974).

MATERIAL
HOLOTYPE: Scale QMF26084 (Fig. 4A-C).
OTHER MATERIAL: Figured scales QMF26085 - 26093 and 124 other scales.

LOCALITY AND HORIZON
Scales occur at eleven localities in the area (SD15, SD128, SD130, SD131, SD146, SD164, SD170, SD196, SD204, SD210, SD216 - Fig. 2), in horizons of the Papilio Formation and its associated Spanner Limestone Member, and the Dosey Limestone, ranging in age from *kockelianus* to *hermanni-cristatus* conodont zones.

DIAGNOSIS
As for genus (this is the only species).

REMARKS
The lateral view of *Gondwanalepis* scales is similar to that of both *Changolepis tricuspidus* Wang, 1984 from the Early Devonian of south-west

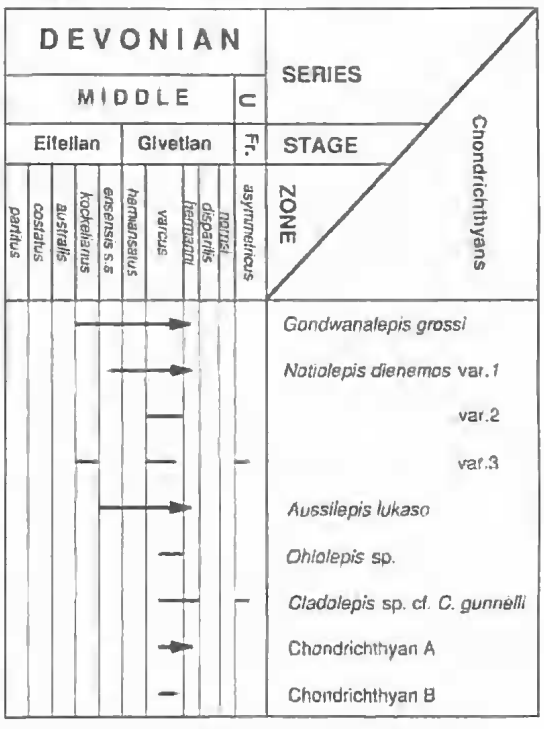


FIG. 3. Relative ranges of chondrichthyan taxa.

China (Wang, 1984: fig. 12f) and *Maplemillia costata* Gross, 1973 from the Late Devonian of Iowa (Gross, 1973: pl. 30 fig. 1d). In all three cases, the gently convex base is flared into a rim around the edge, the neck is deeper at the back, and the crown slopes up and back from the anterior of the base, with no anterior edge on the crown. But *Gondwanalepis* differs from *Changolepis* and *Maplemillia* in the crown ornamentation; neither of these genera has short, parallel ridges on the crown.

The short, deep, parallel ridges on the crown of *Gondwanalepis* are similar to the ornamentation on some acanthodian scales, e.g. *Cheiracanthoides comptus* Wells, 1944 illustrated by Giffin (1980: fig. 5), or *Cheiracanthoides* sp. cf. *comptus* illustrated by Boucot et al. (1989: fig. 19). However, in *Cheiracanthoides* scales the crown is more pointed posteriorly, and the base more convex. The original generic diagnosis for *Cheiracanthoides* of Wells (1944) includes several characters which could be confused with those of *Gondwanalepis*. *Cheiracanthoides* scales have radiating ridges usually extending at least halfway to the posterior corner of the crown, which has a well-defined anterior edge (Wells, 1944: fig. 3). However, the grooves between the ridges are not deep enough to notch the anterior margin deeply, the scales have a well-developed neck, and there are no neck canals. In contrast, scales of *Gondwanalepis* have parallel ridges which are shorter than in *Cheiracanthoides*, the crown has no anterior edge, and the ridges continue down over the front of the scale, where they notch the margin deeply. The neck is not well-developed, being indented only at the posterior. In addition, *Gondwanalepis* scales always lack the concentric ridges on the base, which are typical of acanthodian scales (Gross, 1973).

MEASUREMENTS

The scales vary in length between 0.3mm and 0.8 mm, and in height between 0.3mm and 0.7 mm. The width of most scales is between 0.6mm and 0.8mm, but the range extends from 0.45mm to 1.1mm. The length/width ratio ranges from 0.5 in the particularly wide, high scales with the subrectangular, concave base, to 1.0 in the relatively longer scales with the diamond-shaped, convex base. Approximately 75% of the scales in the available sample have width greater than length. The remaining scales have equal width and length.

DESCRIPTION

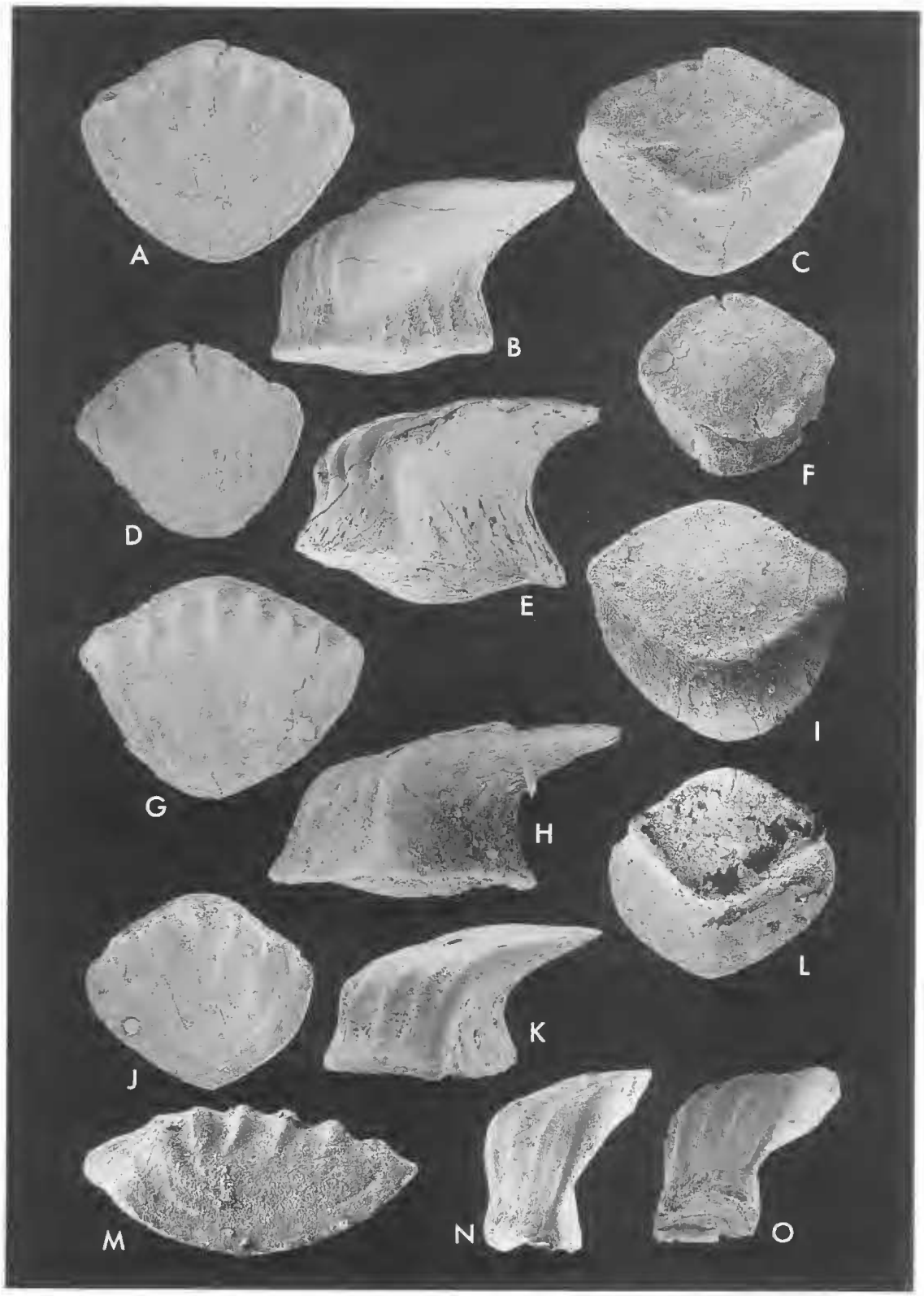
Morphology. The crown bears eight short subparallel ridges. The ridges deeply dissect the anterior edge of the crown, extending down almost to the flared rim around the base. In some particularly wide specimens, with a gently curved anterior margin, the ridges are extremely deep, and give the edge of the scale a scalloped appearance (Fig. 4M-O). The anterior edge of the scale is variably curved, ranging from approximately 90° to 150°. Only 4% of the scales in the available sample have the anterior edge gently curved (Fig. 4M-O); 60% of the scales have the anterior edge moderately curved (Fig. 4A-C, G-I); the remaining scales (36%) have a more sharply curved anterior margin (Fig. 5A-C).

The central ridges extend back from the anterior margin for about one-third the length of the crown. The outer ridges continue as low, narrow curved ridges parallel to the lateral and posterior margins of the crown (Fig. 4A). There may be up to four of these concentric ridges in the posterior section. The anterior margin of the crown is high; the crown slopes slightly upwards posteriorly and extends only a short way beyond the posterior of the base (Fig. 4B,E).

The neck is not clearly defined, although all scales are high, particularly those that are wider than they are long. The neck area is indented posteriorly, and shows up to 12 elliptical canal openings (Fig. 5M,6C). A single row of small circular openings around the lower part of the

FIG. 4. *Gondwanalepis grossi* gen. et sp.nov. A-C, holotype, scale QMF26084 from SD164/19; D-F, scale QMF26085 from SD216/106,1; G-I, scale QMF26086 from SD164/18; J-L, scale QMF26087 from SD128/212 (50 paces north); M-O, scale QMF26088 from SD128/210. A, crown view, x60; B, lateral view, x 95; C, basal view, x 60; D, crown view, x 50; E, lateral view, x 75; F, basal view, x 45; G, crown view, x 45; H, lateral view, x 70; I, basal view, x 45; J, crown view, x 60; K, lateral view, x 90; L, basal view, x 60; M, crown view, x 75; N, lateral view, x 90; O, latero-basal view, x 90.

FIG. 5. *Gondwanalepis grossi* gen.et sp.nov. A-C, scale QMF26089 from SD204/174; D-F, scale QMF26090 from SD164/18; G-I, scale QMF26091 from SD210/9; J-M, scale QMF26092 from SD204/168. A, crown view, x 55; B, lateral view, x 65; C, basal view, x 50; D, crown view, x 50; E, lateral view, x 90; F, basal view, x 60; G, crown view, x 60; H, lateral view, x 75; I, basal view, x 50; J, crown view, x 40; K, lateral view, x 60; L, basal view, x 40; M, posterior view, x 50.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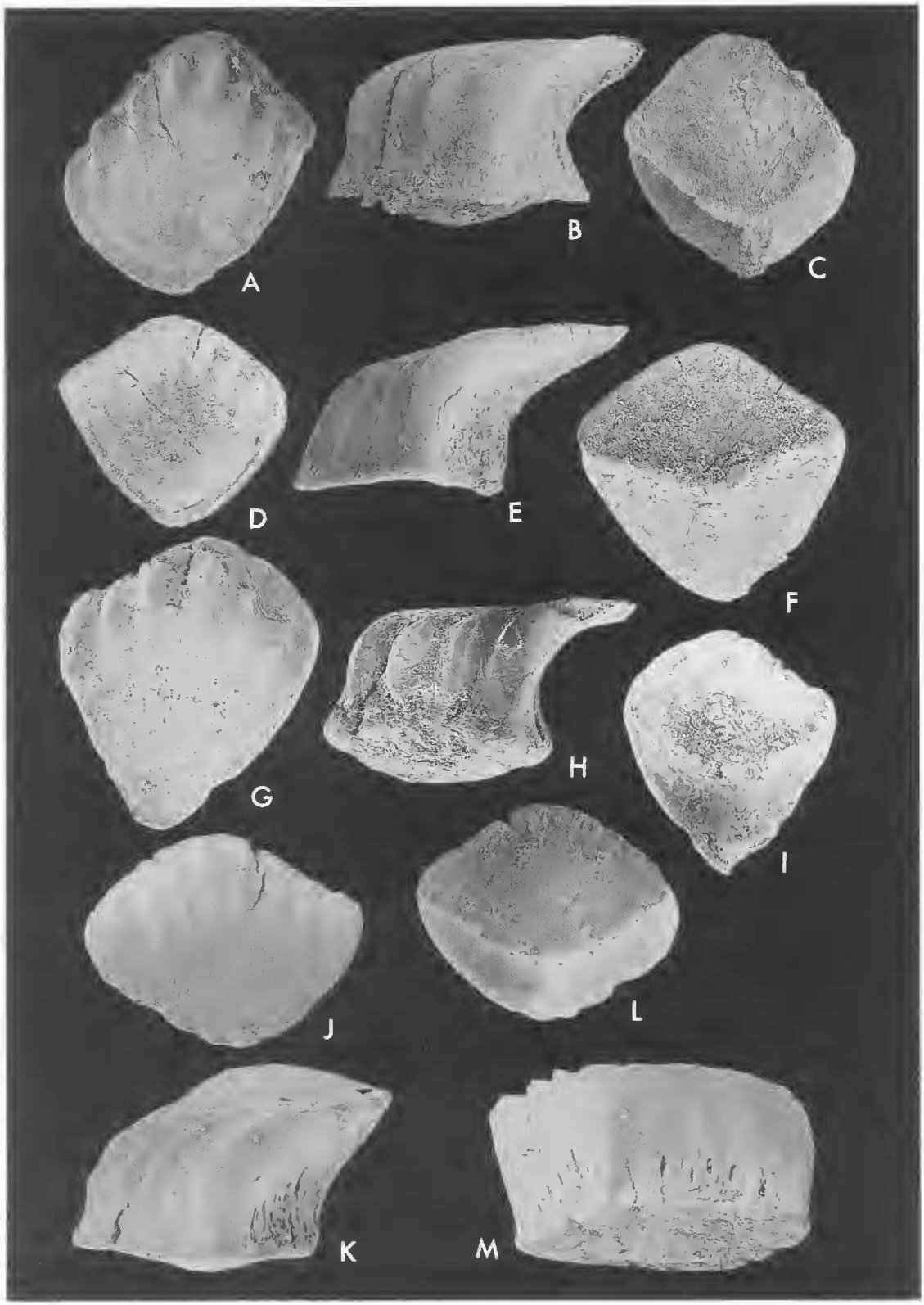
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anterior neck area is visible in some specimens (Fig. 6A).

The base is most commonly diamond-shaped (Fig. 4C, F, I,L), but may be subrectangular (Fig. 4N-O). These represent the ends of a continuous range of morphological types. The diamond-shaped bases are usually gently convex, or sometimes flat, and flared into a narrow rim around the edges. The subrectangular bases are gently concave. All the scales are high relative to the crown area, but this is particularly noticeable in those specimens with the concave, subrectangular base (Fig. 4N-O).

Histology. The base of cellular bone extends in an inverted cone shape high into the scale (Figs 11A,B). This tissue contains osteocytes aligned both concentrically and radially (Fig. 11B). The crown appears to consist of discrete increments added anteriorly and posteriorly to a central initial element (arrow in Fig. 11C). This type of apposed growth is typical of complex chondrichthyan scales (Zangerl, 1981), in contrast to the concentric growth pattern in most acanthodian scales (Dension, 1979); one exception is the acanthodian *Nostolepis robusta* (Brotzen), 1934 described by Gross (1971a) - these scales show some apposition of crown elements. The posterior section of the crown consists of cellular material (Fig. 11D) similar in appearance to the Stranggewebe in acanthodian climatiid scales such as *Cheiracanthoides comptus* Wells, 1944 (e.g. Gross, 1973: fig. 5b,c). This nostolepid-type histology typical of climatiids is also seen in some early cladolepid chondrichthyans (J. Vergoossen, pers. comm., 1994).

DISCUSSION

It is possible that differently shaped scales are of different ages, or occur on different parts of the body. The wide, short scales (Fig. 4M) have a similar width range to the longer scales (Figs 4A,D, 5G). Complex shark scales grow by adding new growth elements around the margins (Zangerl, 1981); it is conceivable that the scale depicted in Fig. 4M is a young scale that could have grown further by additions at the anterior and posterior (see discussion of histology above), resulting in a scale with a more curved anterior margin, longer anterior ridges on the crown, and a longer posterior section to the crown (Figs 4A-C, 4G-I, 5G-I).

Notiolepis gen. nov.

ETYMOLOGY

From the Greek 'notios' = southern, and 'lepis' = scale.

DIAGNOSIS

Crown oval or subrectangular, bearing four to eight parallel anterior ridges. Crown joins directly onto base anteriorly, and slopes up towards posterior. Neck not indented, and has six to twelve canal openings along posterior. Base rhombic or suboval, flat or concave, with no rim around the edge.

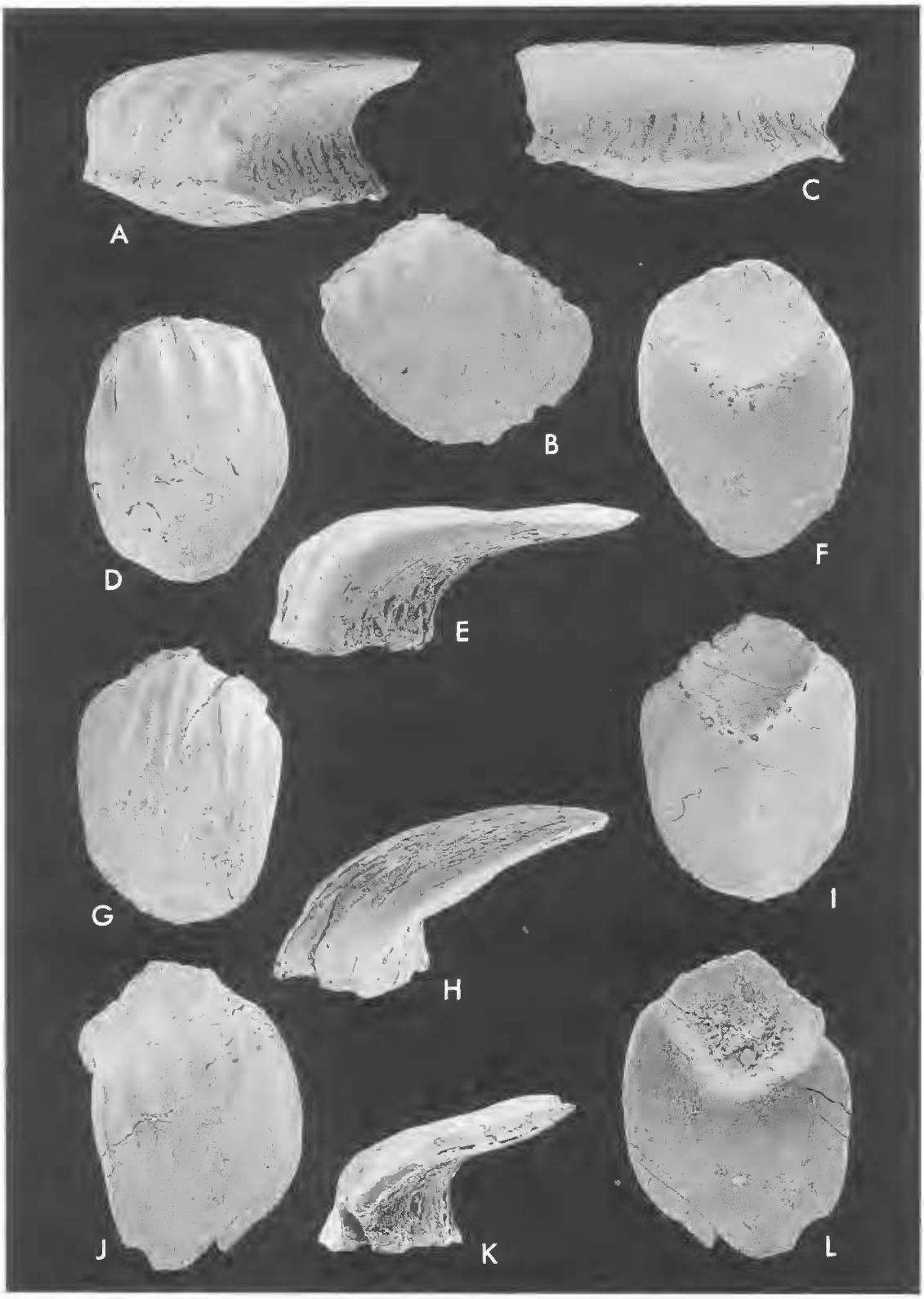
REMARKS

The scales of *Notiolepis* are distinguished from those of *Gondwanalepis*, described above, by the following characters: the crown is relatively longer compared with the width; the anterior ridges on the crown are less pronounced; the neck has the same thickness as the base, rather than being indented as in *Gondwanalepis* ; and the base lacks a rim around its edge. These seem to be consistent differences, even though there is variation in crown shape within each genus, which may indicate scales from different parts of the body. On the available small sample, *Notiolepis* is therefore considered to be a separate taxon, although this assessment may change as more material becomes available.

Notiolepis gen. nov. as defined here may be distinguished from previously described genera in the type of crown ornamentation: the six genera

FIG. 6. A-C, *Gondwanalepis grossi* gen.et sp.nov., scale QMF26093 from SD204/174; D-L, *Notiolepis dienemos* gen.et sp nov. Var. 1. D-F, holotype, scale QMF26094 from SD15/81; G-I, scale QMF26095 from SD204/119.5; J-L, scale QMF26096 from SD204/174. A, lateral view, x 75; B, crown view, x 50; C, posterior view, x 65; D, crown view, x 45; E, lateral view, x 65; F, basal view, x 50; G, crown view, x 50; H, lateral view, x 65; I, basal view, x 50; J, crown view, x 90; K, lateral view, x 90; L, basal view, x 90.

FIG. 7. A-J, *Notiolepis dienemos* gen.et sp.nov. Var. 2; K-M, *Cladolepis* sp. cf. *C gunnelli*. A-D, scale QMF26097 from SD128/212+ (150 paces N) - specimen broken during SEM photography; E-G, scale QMF26098 from SD128/217; H-J, scale QMF26099 from SD128/202.3; K-M, scale QMF26100 from SD190/60. A, crown view, x 55; B, basal view, x 60; C, posterolateral view, x 75; D, detail of broken edge, x 275; E, crown view, x 70; F, lateral view, x 75; G, basal view, x 70; H, crown view, x 55; I, lateral view, x 60; J, basal view, x 55; K, crown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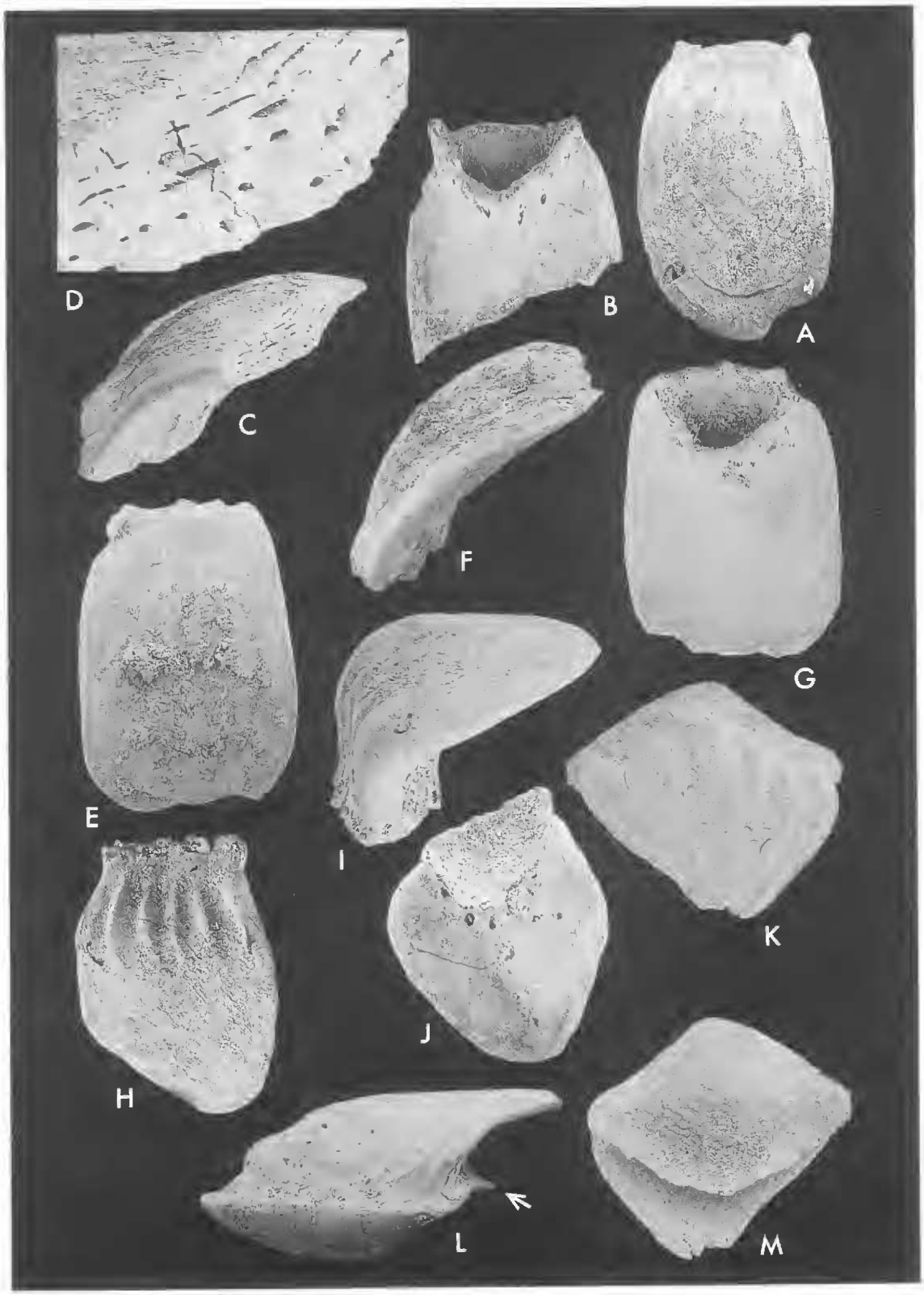
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described and illustrated by Wells (1944); *Cladolepis, Ohiolepis, Deirolepis, Ctenacanthus, Cladoselache,* and *Cladodus*; *Hercynolepis* and *Protacrodus* described and illustrated by Gross (1973); *Polymerolepis* figured by Obruchev & Karatajüte-Talimaa (1967) and Turner & Murphy (1988); *'Skamolepis'* (Giffin, 1980; Turner, 1993); *Ellesmereia* and *Pruemolepis* (Vieth, 1980; Vieth-Schreiner, 1983); *Antarctilamna* (Young, 1982); the three genera from China, *Gualepis, Changolepis,* and *Peilepis* (Wang, 1984); and the Spanish *Iberolepis* and *Lunalepis* (Mader, 1986). No scales of these genera have the short, parallel ribs on the anterior section of the crown, with the posterior part of the crown smooth, as in *Notiolepis*. *Notiolepis* also differs from most of these other chondrichthyan genera in lateral and basal views. *Notiolepis* scales have a similar lateral view to scales of *Ctenacanthus costellatus* Traquair, 1884, *Peilepis solida* Wang, 1984, and *Iberolepis aragonensis* Mader, 1986; the differences between *Notiolepis* and these genera are discussed below.

Notiolepis dienemos sp.nov.
(Figs 6D-L; 7A-J; 8A-F)

ETYMOLOGY

From the Greek 'dienemos' = windswept, referring to the appearance of the crown.

MATERIAL

HOLOTYPE: Scale QMF 26094 (Fig. 6D-F).

OTHER MATERIAL: Variety 1: Figured scales, QMF26095 & 26096, and 24 other scales.

Variety 2: Figured scales, QMF26097-9, and seven other scales.

Variety 3: Figured scales, QMF26101-2, and five other scales.

LOCALITY AND HORIZON

All specimens were recovered from the Papilio Formation, Spanner Limestone or Stanley Limestone. Variety 1 occurred at five localities (SD15, SD128, SD204, SD210, SD216 – Fig. 2) in horizons ranging in age from mid- *ensensis* to *hermanni-cristatus* conodont zones; Variety 2 at two localities (SD128, SD210) in *varcus* Conodont Zone; and Variety 3 at five localities (SD15, SD128, SD192, SD204, SD210) in *kockelianus*, lower and middle *varcus*, and *asymmetricus* conodont zones.

DIAGNOSIS

As for genus (only species).

MEASUREMENTS

Variety 1: scale length varies between 0.5mm and 0.9mm; width ranges from 0.4mm to 0.7mm; height ranges from 0.2mm to 0.3mm. The length/width ratio is 1.17 to 1.29.

Variety 2: length of the crown ranges from 0.7mm to 0.9mm, and width from 0.5mm to 0.6mm. The length/width ratio ranges from 1.4 to 1.6.

Variety 3: the crown length is 0.6mm to 0.7mm, the width is 0.7mm to 0.8mm, and the length/width ratio is 0.86 to 0.87.

DESCRIPTION

Morphology. Three varieties of scales have been grouped together on the basis of their similar lateral views (Figs 6E,H,K; 7F,I; 8B,E).

In Variety 1, (Fig. 6D-L), the crown is oval shaped, with both anterior and posterior edges gently curved. The crown bears four to seven long parallel ridges, usually starting at the anterior edge and extending posteriorly approximately half to two-thirds the length of the crown. In some specimens, the base extends slightly anteriorly, to give a smooth anterior margin to the scale in dorsal view (Fig. 6J). In these specimens, the parallel ridges do not extend right to the anterior margin of the scale, and the crown extends further beyond the base posteriorly than in the specimens lacking the anterior basal extension. The base is diamond- shaped, and either flat or gently concave. Up to 12 neck canal openings are found at the posterior.

In Variety 2 (Fig. 7A-J) the crown is subrectangular, thin, and slopes steeply upward from a fairly straight anterior edge to a gently rounded posterior margin. The crown bears four to seven parallel ridges, extending from just behind the anterior edge, back to approximately mid-way towards the posterior (Fig. 7E,H). The neck area is not indented. The base is a concave, narrow semi-diamond or semi-oval shape, and, like the crown, is straight along the anterior margin (Fig. 7B,G). The general appearance of the scale is wide, flat and high, with only the base area appearing to have much volume. Specimen QMF26097 was broken during SEM photography, revealing numerous pulp canals within the crown (Fig. 7D), typical of the composite type of chondrichthyan scale described by Zangerl (1981), where each new growth element has its own vascular supply.

Variety 2 scales mainly differ from those of Var. 1 in their base. The base of Var. 1 scales is flat or gently concave, and diamond-shaped. The

TABLE 2. Reported chondrichthyans from the Early and Middle Devonian of Australia.

Taxa	Locality	Age	Material	Reference
Antarctilamna sp.	Bunga Beds	Late Giv. - early Fras.	teeth, fin spines, scales,dermal denticles, endocrania& jaw	Young, 82; Long, 91; Turner, 91; 93
cf. *Gualepis*	Cravens Peak		scales	Turner, 91; 93
?*Mcmurdodus* cf. *featherensis*	Bunga Beds	Late Giv. - early Fras.	teeth	Young, 82
Mcmurdodus whitei	Cravens Peak	Eifelian	teeth	Turner & Young, 87; Turner, 93
Ohiolepis sp.	Jerula Fm., Trundle Beds, Dulladerry Rhyolite, Mt. Dam Limestone	Lochkovian		Turner, 93
	Tumblong	Pragian	denticles	Pickett et al., 85
	Tumblong	Emsian		Turner, 93
	Receptaculites Limestone	? Late Emsian	scales	Giffin, 80
	Murrum & Buchan Lsts.	Late Ems. - early Fras.	scales	Turner, 82
	Mt. Frome Limestone	*serotinus/patulus* Zones - early Eifelian		Turner, 93
	Taemas - Buchan	Emsian (*dehiscens - serotinus*)		Young, 93
'*Skamolepis*' sp.	*Receptaculites* Limestone	Late Emsian	scales	Giffin, 80
	Jesse Limestone	Late Emsian (*perbonus - laticostatus*)	scales	Turner, 93
	Mt. Frome Limestone	*serotinus - patulus* Zones	scales	Turner, 93
Xenacanthus sp.	Bunga Beds	Late Givetian - Early Frasnian	teeth	Young, 82
Possible occurrences:				
cf. *Antarctilamna*	Silverband Fm., Grampians	Gedinnian - early Frasnian	scales, fin spines, tooth whorls	Turner, 86
Neoselachian-like	Trundle Beds	?Late Lochkovian	scale	Turner, 91; 93
shark	Bunga Beds	Mid Devonian	articulated or semi-articulated cartilage remains	Long, 91
possible shark	Buchan Gp. & Pt. Hibbs Lst.	Pragian	scales	Turner, 93

base of Var. 2 scales is deeply concave, and a narrow half-diamond or semi-oval shape, with the anterior edge of the base fairly straight.

In Variety 3 (Fig. 8A-F) the crown is fairly straight across the anterior, but rounded at the posterior (Fig. 8D). The front of the crown slopes up steeply from the base, then levels out and slopes up more gradually towards the posterior margin (Fig. 8B). Seven short parallel ridges occur on the steeply sloping anterior edge of the crown. The posterior part of the crown is flat, thin and unornamented. The neck is not constricted. The base is a flat, narrow rhombic shape (Fig. 8C,F). Six to eight elliptical neck canal openings occur on the underside of the crown, just behind the base. The overall appearance of these scales is wide, flat, and low. The crown is wider than it is long.

Variety 3 scales differ from Var. 1 and Var. 2 in the shape of both the base and the crown. The base here is flat and narrowly rhombic, in contrast with the diamond-shaped flat or gently concave base of Var. 1, and the narrow half-diamond- or semi-oval-shaped deeply concave base of Var. 2. The crown of Var. 3 scales is straight at the anterior edge, widely rounded at the posterior

edge, and bears seven short parallel ridges only at the very front of the scale. The crown of Var. 1 and Var. 2 bears parallel ridges extending much further back towards the posterior. The angle of inclination of the crown varies between individual scales but is similar in all three varieties of *Notiolepis*. However, each of the three varieties has the length/width ratio falling within a distinctive range, reflecting a general difference in overall scale shape between the three varieties: 1.17-1.29 for Var. 1, 1.4-1.6 for Var. 2, and 0.86-0.87 for Var. 3.

Histology. Scales consist of a conical bony base (Fig. 12A), containing osteocytes and fine radial fibres (Fig. 12B). The cellular crown material is attached to the posterior edge of the basal cone (Fig. 12A). The crown, like that of Gondwanalepis, appears to grow by apposition of discrete elements (Fig. 12B), and these crown elements also consist of material similar in appearance to Stranggewebe (Fig. 12C).

DISCUSSION

Notiolepis scales are similar in lateral view to the scales of the chondrichthyans *Ctenacanthus costellatus* Traquair, 1884 (Reif, 1978: fig. 1a), *Peilepis solida* Wang, 1984 (Wang, 1984: figs 14, 15), and *Iberolepis aragonensis* Mader, 1986 (Mader, 1986: pl. 4, fig. 2c). *Notiolepis* scales differ from *C. costellatus* Traquair, 1884 scales by lacking the constricted neck and flared base, and having less pronounced, but a greater number of, anterior ridges on the crown. The *P. solida* Wang, 1984 scales have an anteriorly protruding base, a large basal cavity, a posteriorly bifurcated crown, and three flutings on the anterior crown surface, all of which are absent in *Notiolepis*. The base of *I. aragonensis* Mader, 1986 is longer and flatter than that of *Notiolepis*, and the crown ornamentation is different.

Specimens of *Notiolepis* with the concave base (Var. 1) resemble those of *Antarctilamna prisca* Young, 1982 in basal view (Young, 1982: fig. 4e). However, *Notiolepis* Var. 1 scales differ in having a more gently concave base, lacking a constricted neck, and having parallel ridges in the anterior part of the crown rather than concentric ridges over the whole crown forming short cusps along the posterior margin. Variety 2 scales also have a basal view similar to that of *A. prisca* Young, 1982, except that the concave cup-like base is narrower.

In lateral view, *Notiolepis* scales may perhaps be confused with some thelodont scales, for example *Turinia* sp. (Young et al., 1987: fig. 5b) or *Canonia grossi* Vieth, 1980 (Vieth, 1980: pl. 3, fig. 3c). However, the *Notiolepis* scales lack the thick, rounded base encircling the lower edge of the scale, the large basal cavity and the single pulp canal opening typical of thelodont scales. In addition, the posterior part of the crown is thinner and flatter, and the crown bears ridges only at the anterior edge, not laterally as is the case with the *Turinia* sp. scales figured by Young et al. (1987). Scales of *C. grossi* Vieth, 1980 have a round, gently convex base in ventral view, and three pronounced ridges covering the length of the crown and extending into three denticles at the posterior margin in dorsal view. *Notiolepis* scales, in contrast, have a rhombic, flat or concave base, ridges only in the anterior part of the crown, and a smoothly rounded posterior margin.

Aussilepis gen. nov.

ETYMOLOGY

From the local colloquial word Aussie, and the Greek 'lepis' = scale.

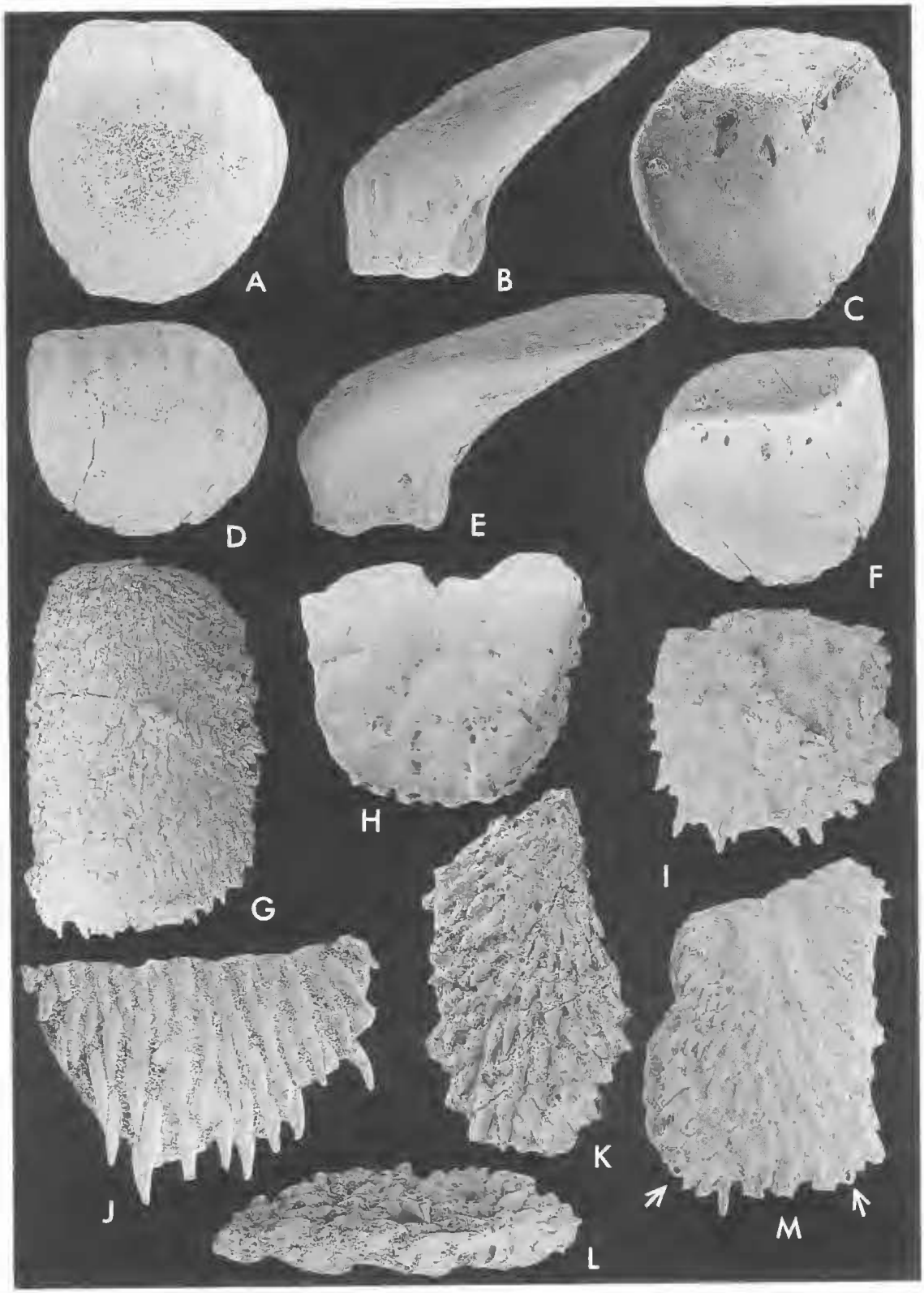
DIAGNOSIS

Crown subcircular, extends beyond base posteriorly. Eight thick, deep ridges extend from anterior edge to approximately middle of crown. Neck shallow, slightly indented at anterior and posterior. Approximately six to ten small openings in posterior part of neck. Base diamond-shaped, convex.

REMARKS

The scales of *Aussilepis* resemble those of *Gondwanalepis* in the deep anterior ridges on the crown, and in the narrow rim around the margin of the base, this latter feature distinguishing these two genera from *Notiolepis*. However, *Aussilepis*

FIG. 8. A-F, *Notiolepis dienemos* gen.et sp.nov. Var. 3; G-M, *Ohiolepis* sp. A-C, scale QMF26101 from SD128/212; D-F, scale QMF26102 from SD204/174; G, scale QMF26105 from SD128/144.2; H, scale QMF31828 from SD204/174 upslope; I, scale QMF26104 from SD216/99.8; J, broken scale QMF31829 from SD204/174 upslope; K,L, scale QMF26103 from SD130/262.5; M, scale QMF31830 from SD204/174 upslope. A, crown view, x 60; B, lateral view, x 85; C, basal view, x 60; D, crown view, x 50; E, lateral view, x 95; F, basal view, x 50; G, crown view, x 25; H, basal view, x 45; I, crown view, x 35; J, crown view, x 60; K, crown view, x 45; L, lateral view, x 60; M, crown view, x 45.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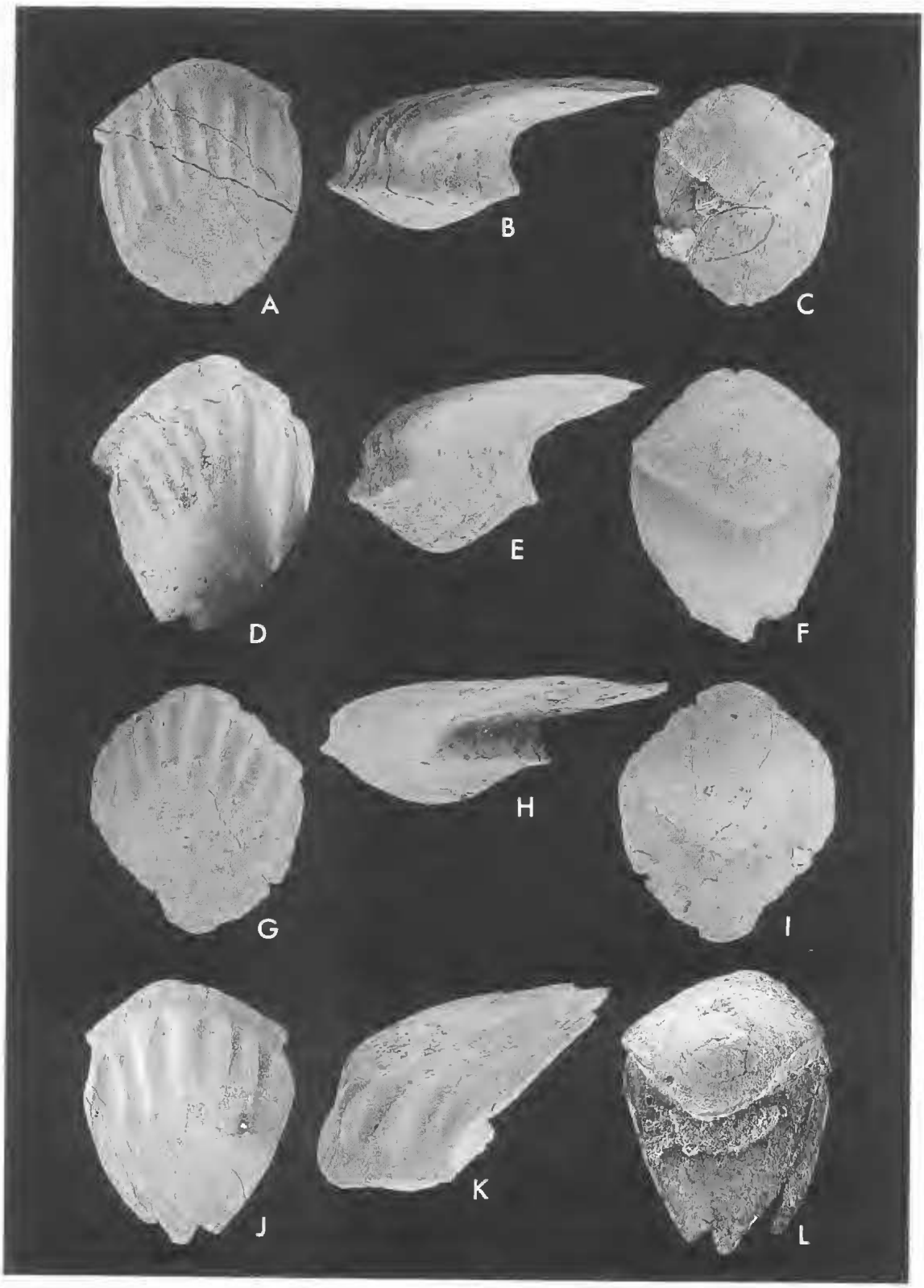
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differs from *Gondwanalepis* in the following features: the posterior part of the crown is smooth, thin, and lacks the narrow ridges parallel to the posterior margin; the crown overhangs the base further posteriorly; the base is more convex; and the outer ridges of the crown are less thickened (Fig. 9B,E,H) in contrast to *Gondwanalepis* (Figs 4B,K; 5E,K).

Aussilepis scales are distinguished from *Notiolepis* scales by the differences in neck and base; *Aussilepis* has a slightly indented neck and convex base, while in *Notiolepis* the neck and base are the same size, with the base being either flat or concave. The base of *Notiolepis* scales occupies a smaller proportion of the length of the scale than with *Aussilepis* scales.

These scales have been assigned to a new genus because their morphology is unlike that of previously described scales (Tables 2, 3). As with *Gondwanalepis* and *Notiolepis*, it is the crown ornamentation that differs most from previously described genera. The crown of *Aussilepis* has short, deep ridges and furrows at the anterior margin, while the posterior section of the crown in unornamented (except for occasional low markings, similar to growth rings, parallel to the posterior margin Fig. 9J). *Cladolepis* scales (Wells, 1944) have a flat, thin crown ornamented by long curved ridges with shorter, overlapping ridges anteriorly. The crown of *Ohiolepis* scales is covered with numerous anteriorly grooved spines (Wells, 1944). *Deirolepis* scales (Wells, 1944) have a long neck and thin base. Scales of *Ctenacanthus, Cladoselache,* and *Cladodus*, as figured by Wells (1944), all lack the anterior parallel ridges present on the crown of *Aussilepis*. The crown of *Hercynolepis* scales is covered with short, backwardly-pointing, slightly overlapping ribs (Gross, 1973). *Protacrodus* scales have a low, flat crown, deeply convex base, and distinct furrow where the base joins the neck area (Gross, 1973). Scales of *Polymerolepis* have the crown ornamented with many deep parallel or radiating ridges (Obruchev & Karatajüte-Talimaa, 1967; Turner & Murphy, 1988). Scales described as *'Skamolepis'* by Giffin (1980) differ from those of *Aussilepis* in general shape and ornamentation. Scales of *Ellesmereia* (Vieth, 1980) have ridges extending from the anterior right to the posterior margin of the crown, and the neck of *Ellesmereia* is more constricted. *Aussilepis* lacks the constricted neck, the concave, cup-shaped base, and distinctive curved ridges on the crown of *Antarctilamna* (Young, 1982), and is thicker in lateral view. *Pruemolepis* scales (Vieth-Schreiner, 1983; Mader, 1986) have a thicker crown, a more constricted neck, and less conspicuous crown ornamentation than those of *Aussilepis*. *Gualepis* (Wang, 1984) is characterised by a constricted neck and a dentate posterior margin. *Changolepis* (Wang, 1984) has a strongly convex central rib on the crown forming a long posterior cusp. The crown of *Peilepis* (Wang, 1984) has anterior flutings and is posteriorly bifurcated, and the flat base has a large elliptical pulp opening. Scales of both *Iberolepis* and *Lunalepis* (Mader, 1986) have parallel ridges extending to the posterior margin of the crown.

Aussilepis lukaso sp.nov.
(Fig. 9)

ETYMOLOGY

From the languages of the Koori (original inhabitants of Australia) 'luk' = like, and 'kaso' = another, referring to the similarity between the lateral view of these scales and that of some other taxa.

MATERIAL

HOLOTYPE: Scale QMF26106 (Fig. 9A-C).

OTHER MATERIAL: Figured scales, QMF26107-9 and 75 other scales.

LOCALITY AND HORIZON

Scales occur at eight localities (SD15, SD128, SD146, SD164, SD196, SD204, SD210, SD216 - Fig. 2), in horizons of the Papilio Formation and its associated Spanner Limestone Member dated from *ensensis* to *hermanni- cristatus* conodont zones.

DIAGNOSIS

As for genus (this is the only species).

MEASUREMENTS

Scales range in length from 0.5mm to 0.9mm; in width from 0.4mm to 0.9mm; and in height from 0.3mm to 0.45mm. The length/width ratio ranges from 1.0 to 1.33.

FIG. 9. *Aussilepis lukaso* gen.et sp.nov. A-C, holotype, scale QMF26106 from SD204/174; D-F, scale QMF26107 from SD204/174; G-I, scale QMF26108 from SD204/174; J-L, scale QMF26109 from SD210/30; A, crown view, x 50; B, lateral view, x 70; C, basal view, x 45; D, crown view, x 50; E, lateral view, x 60; F, basal view, x 50; G, crown view, x 45; H, lateral view, x 60; I, basal view, x 45; J, crown view, x 60; K, lateral view, x 75; L, basal view, x 60.

TABLE 3. Reported chondrichthyans from the Early and Middle Devonian from overseas.

Taxa	Locality	Age	Material	Reference
Antarctilamna prisca	Aztec Siltstone, Antarctica	Givetian	fin spines, scales, teeth	Young, 82; 89; 91
A. seriponensis	Catavi Fm., Bolivia	Late Early - Mid. Devonian	fin spine	Gagnier et al., 88
	Santa Rosa Fm., Bolivia	Lochkovian - Pragian	fin spine	Lelievre et al., 93
Antarctilamna sp.	Wajid Sandstone, Iran	Pragian	scales	Forey et al., 92
	Sicasia & Belen Fms., Bolivia	Mid. Devonian	fin spine	Lelievre et al., 93
	Khush - Yeilagh Pass, Bolivia	Emsian - Eifelian	fin spine	Lelievre et al., 93
Arauzia federicoi	Spain	Early Devonian	scales	Mader, 86
Bolivacanthus sagitalis	Catavi Fm., Bolivia	Late Early - Mid. Devonian	spine fragment	Gagnier et al., 88
	Santa Rosa Fm., Bolivia	Lochkovian - Pragian	fin spine	Lelievre et al., 93
Changolepis tricuspidus	Xitun Member, Sth China	Early Devonian	scales	Wang Nianzhong, 84
Cladodus (Protacrodus) wildungensis	Cincinnati Arch region, US	Mid. Devonian	scale	Wells, 44
Cladolepis gunnelli	Cincinnati Arch region, US	Mid. Devonian	scales	Wells, 44
	Indiana, US	Early Mid. Devonian	scales	Gross, 73
?C. gunnelli	Lauch Fm., Germany	Early Eifelian	scale	Vieth - Schreiner, 83
C. ornata	Cincinnati Arch region, US	Mid. Devonian	scale	Wells, 44
Cladolepis sp.	Spain	Early Devonian	scales	Mader, 86
Cladoselache fyleri	Cincinnati Arch region, US	Mid. Devonian	scale	Wells, 44
Ctenacanthus clarki	Cincinnati Arch region, US	Mid. Devonian	scale	Wells, 44
Ctenacanthus sp.	Pimenteira Fm., Brazil	Mid. Devonian	fin spine	Janvier & Melo, 92
	Iran	Late Givetian - Early Frasnian		Lelievre et al., 93
Deirolepis carinatus	Cincinnati Arch region, US	Mid. Devonian	scale	Wells, 44
Ellesmereia schultzei	Arctic Canada	Early Devonian	scales	Vieth, 80
Gualepis elegans	Xitun Member, South China	Early Devonian	scales	Wang Nianzhong, 84
Hercynalepis meischneri	Harz	Early Devonian	scales	Gross, 73
?H. meischneri	Spain	Early Devonian	scale	Mader, 86
Iberolepis aragonensis	Spain	Early Devonian	scales	Mader, 86
Leonodus carlsi	Spain	Early Devonian	teeth	Mader, 86
L. cf. L. carlsi	Belgium	Early Devonian	teeth	Blieck & Goujet, 91
Lunalepis leonensis	Spain	Early Devonian	scales	Mader, 86
Mcmurdodus feotherensis	Aztec Siltstone, Antarctica	Givetian	teeth	Young, 91
Ohiolepis newberryi	Cincinnati Arch region, US	Mid. Devonian	scales	Wells, 44
	Ohio & Indiana, US	Early Mid. Devonian	scales	Gross, 73
	Sotenich Trough, Germany	Eifelian	scales	Friman, 83
	Lauch Fm., Germany	Early Eifelian	scales	Vieth-Schreiner, 83
	Spain	Early Devonian	scale	Mader, 86
O. frohnrathensis	Sotenich Trough, Germany	Early Eifelian	scales	Friman, 83
?O. xitunensis	Xitun Member, South China	Early Devonian	scales	Wang Nianzhong, 84
Ohiolepis sp.	Heisdorf Beds, Germany & New York state, US	Emsian - Eifelian		Ørvig, 69

TABLE 3. Continued.

Taxa	Locality	Age	Material	Reference
Peilepis solida	Xitun Member, South China	Early Devonian	scale	Wang Nianzhong, 84
Phoebodus floweri	Cincinnati Arch region, US	Mid. Devonian	teeth	Wells, 44
	Indiana, US	Early Mid. Devonian	teeth	Gross, 73
?Ph. bryanti	Cincinnati Arch region, US	Mid. Devonian	teeth	Wells, 44
	Iowa, US	Early Mid. Devonian	tooth	Gross, 73
Polymerolepis whitei	Dneister Range, Podolia	Early Devonian	scales	Orbruchev & Karatajute-Talimaa, 67
	Simpson Park Range, Nevada	Lochkovian (*delta* Zone)	scales	Turner & Murphy, 88
Protacrodus wellsi	Iowa, US	Early Devonian	scales	Gross, 73
Protacrodus sp.	Harz & Morocco	Early Devonian	scales	Gross, 73
	Germany & US	Mid. - Late Devonian		Zangerl, 81
	Iran	Late Givetian - Early Frasnian		Lelievre et al., 93
Pruemolepis wellsi	Lauch, Helsdorf & Wetteldorf Fms., Germany	Emsian - Eifelian	scales	Veith - Schreiner, 83
Pruemolepis sp.	Spain	Early Devonian	scales	Mader, 86
Pucapampella rodrigae	Sicasica & Belen Fms., Bolivia	Eifelian	synarcual	Lelievre et al., 93
Zamponiopteron falciformis	Sicasica & Belen Fms., Bolivia	Devonian		Lelievre et al., 93
Z. triangularis	Sicasica & Belen Fms., Bolivia	Devonian	fin element	Lelievre et al., 93
Z. spinfera	Sicasica & Belen Fms., Bolivia	Devonian		Lelievre et al., 93
Possible occurrences:				
Indet scale	Vestspitsbergen	Emsian - Eifelian	scale	Ørvig, 69
Pleuracanth	Bokkeveld Gp., South Africa	Late Mid. Devonian	tooth impressions	Oelofsen, 81
Chondrichthyan ?	Catavi Fm., Bolivia	Late Early - Mid. Devonian	spines	Gagnier et al., 88
Indet shark scale	Simpson Park Range, Nevada	Lochkovian (*delta* Zone)	scale	Turner & Murphy, 88
Xenacanthid sp. nov. & others	Aztec Siltstone, Antarctica	Givetian	teeth	Young, 89; 91
Chondrichthyan	Talengit sequence	Emsian		Lelievre et al., 93

DESCRIPTION

Morphology. In these scales the subcircular crown extends posteriorly beyond the base such that the length of the base is approximately half to two-thirds the length of the crown (Fig. 9C,F,I,L). The parallel ridges on the crown become thinner and shallower posteriorly, and disappear at about the middle of the crown. The crown has no anterior rim; rather the ridges extend down the anterior edge of the crown and neck, ending just above the flared joint of neck area and base (Fig. 9K). The neck is shallow, in some specimens slightly deeper posteriorly (Fig. 9B,E), with only very slight anterior and posterior indentations in lateral view. The neck area is not indented laterally. Six to ten small round neck canal openings are located in the posterior neck area (Fig. 9E). The convex base is diamond-shaped, and flared into a slight rim around the perimeter, where it connects with the neck (Fig. 9B,E,H). In some specimens the base extends anteriorly beyond the crown, producing a smooth anterior margin on the scale (Fig. 9A,D). Such scales are deeper in a dorso-ventral direction.

Histology. The conical bony base contains both fine radial fibres (Fig. 13A) and osteocytes (Fig.

13B). The crown shows no evidence of concentric growth but, like both *Gondwanalepis* and *Notiolepis*, consists of apposed increments of Stranggewebe-like material (Fig. 13B).

DISCUSSION

The basal view of *Aussilepis lukaso* is similar to that of the Late Silurian shark *Elegestolepis grossi* Karatajüte-Talimaa, 1973 (Karatajüte-Talimaa, 1973: pl. 3, figs 3b, 4b). However, the crown ornamentation of the two types of scale is quite different; the ridges on *Elegestolepis* are longer, thinner, and more numerous than those on *Aussilepis*.

Some of the scales, in lateral view, are similar to illustrated acanthodian scales, for example *Nostolepis striata* Pander, 1856 (Gross, 1947: pl. 25 fig. 7c; Denison, 1979: fig. 17f), *N. arctica* Vieth, 1980 (Vieth, 1980: pl. 5, figs 4b, 5b, 7b), *Cheiracanthoides comptus* Wells, 1944 (Gross, 1973: pl. 27, fig. 2c), or *Cheiracanthoides* sp. cf. *comptus* (Boucot et al., 1989: fig. 19a).

Apart from the absence of neck canal openings, these scales differ from *Aussilepis* in various morphological details. *Nostolepis* scales have a posteriorly pointed crown ornamented with converging ridges, commonly paired, with a median depression (Denison, 1979; Forey et al., 1992). However, the crown of *Aussilepis* scales is rounded posteriorly, and extends further beyond the base posteriorly than in the acanthodian scales. The base of *Aussilepis* is less strongly convex than the base of *Nostolepis* scales (Gross, 1947: pl. 26; Forey et al., 1992: fig. 12a).

In scales of *Cheiracanthoides comptus* Wells, 1944, the grooves between the ridges are not deep enough to notch the anterior margin (Wells, 1944). In *Aussilepis* scales, the anterior edge of the crown is always deeply notched (Fig. 9K), as is also the case with *Gondwanalepis*. Scales of *C. comptus* Wells, 1944 have a constricted neck, unlike those of *Aussilepis*, and a nearly flat crown. *Aussilepis* scales have a crown that slopes down anteriorly to meet the flared rim joining the base and neck; there is no anterior rim to the crown of *Aussilepis* as there is in *Cheiracanthoides*. Scales of *C. comptus* Wells, 1944 have a 'thick, inflated' base (Wells, 1944), described by Gross (1973) as "highly domed". The base of *Aussilepis* scales is convex, but more gently so than in figured scales of *C. comptus* Wells, 1944, and appears smooth, lacking the distinct concentric striations characteristic of acanthodian scales (Gross, 1973). As with *Nostolepis striata* Pander, 1856 (Denison, 1979: fig. 17f), the crown of *C. comptus* Wells, 1944 extends posteriorly beyond the base a shorter distance than in *Aussilepis*.

Ohiolepis Wells, 1944

TYPE SPECIES

Ohiolepis newberryi Wells, 1944

Ohiolepis sp.
(Fig. 8G-L)

REMARKS

The genus *Ohiolepis* was established by Wells (1944) for scales from the Middle Devonian bone beds of Ohio, Indiana, and Kentucky. His two species, *O. newberryi* and *O. stewartae*, were subsequently united by Gross (1973), who ascribed differences in shape between the two species to scales coming from different parts of the body. The taxon has also been reported from Australia (Schultze, 1968; Giffin, 1980; Turner, 1982; Pickett et al., 1985; Turner, 1993; Young, 1993), China (Wang, 1984), and Germany (Ørvig, 1969; Friman, 1983; Vieth-Schreiner, 1983); see Tables 2, 3. Turner (1993) questioned the chondrichthyan affinities of some of these records, suggesting that some might be placoderm scales.

Two new species have been erected since Gross's 1973 amalgamation: '*Ohiolepis*' *frohnrathensis* Friman, 1983 from the early Eifelian of Germany, and *O.? xitunensis* Wang, 1984 from the Early Devonian of China. All other occurrences have been assigned either to *O. newberryi* or simply to the genus.

Scales assigned to the genus and figured in the literature vary in morphology. Wells (1944) established as generic characters a flat or convex base; a broad crown ornamented by numerous spines that are enamelled, anteriorly indented or grooved, with an anterior sloping face, acute posteriorly inclined tips, and resting directly on the base; and a narrow, spine-free strip around the anterior edges and sides of the scale. However, Wells (1944:38) also remarked that the spines of *O. newberryi* Wells, 1944 may be blunt and club-shaped; this is inconsistent with his diagnosis. Wells described his less common second species, *O. stewartae*, as having spines similar to those of *O. newberryi* Wells, 1944, but fewer in number, and arranged in a single transverse series with the smallest spine in the centre.

Gross (1973) placed the two species in *O. newberryi* Wells, 1944 by combining Wells's two

groups of specific characters, but made no mention of the spines being blunt or club-shaped, or having an anterior groove. However, his illustrations show scales with both pointed (Gross, 1973: pl. 30, figs 8-21) and blunt-tipped (pl. 31, fig. 8) spines, and both with (pl. 30, figs 8-21) or without (pl. 31, figs 6,7) an anterior groove. Most of Gross's figures (1973: pl. 30, figs 8-19,21; pl. 31, figs 3-7) show examples similar to Wells's original *O. newberryi* type, with numerous closely- packed spines, each having an anterior groove and a posteriorly-directed acute tip. Other examples (Gross, 1973: pl. 31, figs 1, 2) have the spines more widely-spaced and conform more closely to Wells's original description for *O. stewartae*. Indeed, all specimens of *Ohiolepis* described since 1973 have widely-spaced spines (Giffin, 1980: fig. 4a,b; Friman, 1983: figs 1,2; Vieth-Schreiner, 1983: pl. 4, fig. 36; Wang, 1984: figs 16,17; Pickett et al., 1985: cover photo K). On this evidence, it seems best for the moment to provisionally retain Wells's two species, with *O. newberryi* only known from North America, and examples from elsewhere showing more resemblance to *O. stewartae*. In the absence of precise locality data, it is possible that the material analysed by Gross came from several different horizons.

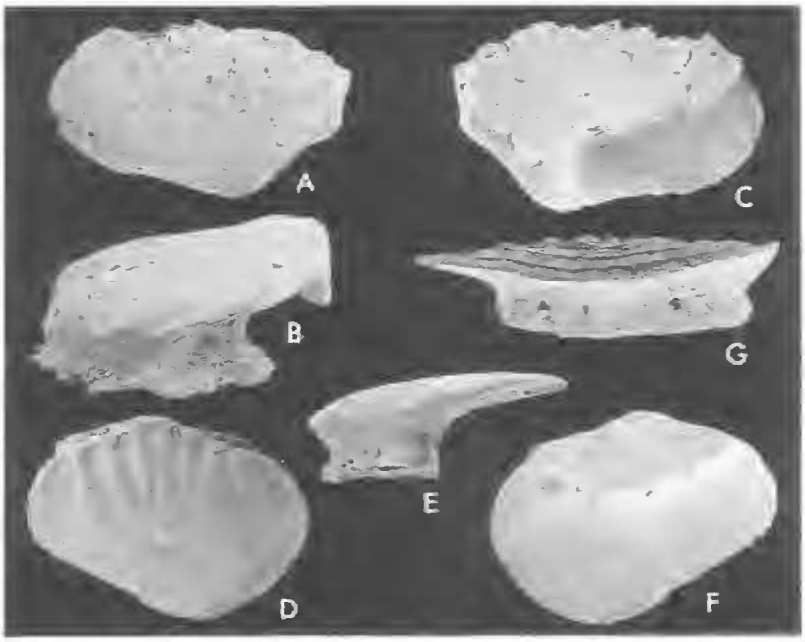

FIG. 10. A-C, Chondrichthyan A - fam.,gen. et sp. indet., scale QMF26110 from SD15/192; D-G, Chondrichthyan B - fam.,gen. et sp. indet., scale QMF26111 from SD204/174. A, crown view, x 32; B, lateral view, x 56; C, basal view, x 32; D, crown view, x 48; E, lateral view, x 72; F, basal view, x 48; G, posterior view, x 68.

The concept of the genus *Ohiolepis* is further confused because one of Friman's (1983) species characters for *'Ohiolepis' frohnrathensis* is inconsistent with Wells's (1944) genus diagnosis: *'Ohiolepis' frohnrathensis* Friman, 1983 scales lack an anterior groove on the spines. One option is to consider anterior grooves on the spines a generic character applying to most scales in a sample, but accepting some variation in scales from different regions of the body. Friman's specimens (1983: fig. 2b-e) have spines on the crown not dissimilar to those found on dermal denticles from the branchial region of *Antarctilamna prisca* Young, 1982 (fig. 2c,d; pl. 87, figs 9,10), so this morphotype might occur in many different shark taxa.

Wang's (1984) *O.? xitunensis* was provisionally referred to *Ohiolepis*. Listed differences between *O. newberryi* Wells, 1944 and his new species included shape of the denticles, and shape and structure of the base.

MATERIAL

Six scales; QMF26103-5, QMF31828-30 (Fig. 8G-M).

LOCALITY AND HORIZON

The scales occur in four sections of the Broken River Group (SD128, SD130, SD204 and SD216 - Fig. 2), in horizons of the Papilio Formation and the associated Spanner Limestone Member aged middle and upper *varcus* Conodont Zone. This age is younger than other occurrences of *Ohiolepis*; both Ørvig (1969) and Friman (1983) consider the genus to be characteristic of Emsian/Eifelian boundary beds in Europe, North America, and Australia.

MEASUREMENTS

The scales range in length from 0.7mm to 2.5mm, and in width from 0.7mm to 1.6mm.

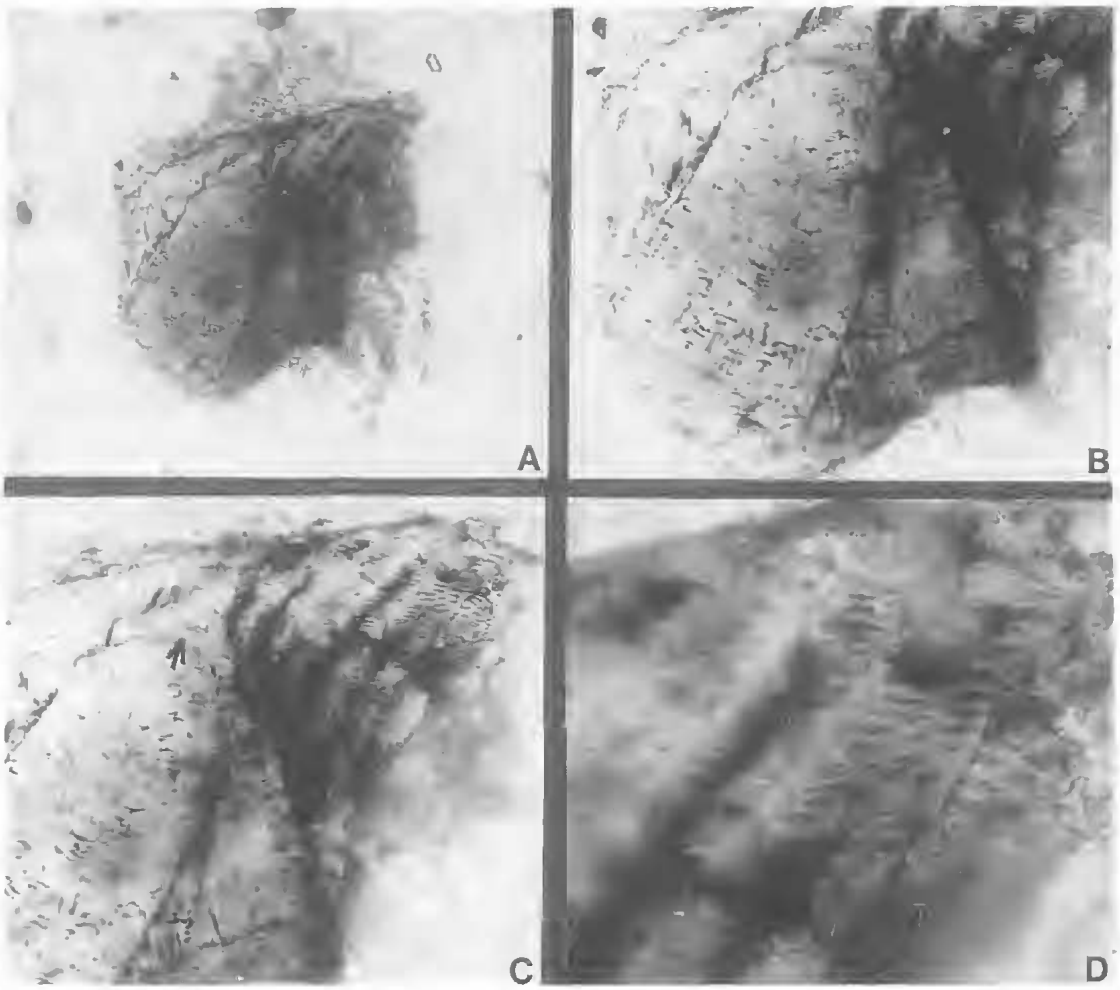

FIG. 11.*Gondwanalepis grossi* gen.et sp.nov., longitudinal section QMF26112 of scale from SD204/174 upslope. A, full view, x 30; B, detail of base, x 60; C, detail of posterior part of scale, x 60; D, detail of posterior part of crown, x 180.

DESCRIPTION AND DISCUSSION

With only six scales, the examples from Broken River can only be provisionally compared with *Ohiolepis*. Each has a crown completely covered with numerous small, conical, closely-packed, posteriorly inclined tubercles or spines, without an anterior groove (Fig. 8G,I,J,K,M). The spines radiate from the centre anterior margin (Fig. 8G,M) and cover the crown, although one specimen (Fig. 8M) has a small spine-free area in the central anterior region of the crown. Broken spines (arrows in Fig. 8M) show a central cavity. The scales have a subcircular to subrectangular outline, a very shallow neck, and a flat or slightly concave unornamented base (Fig. 8H).

The crown of these new scales has spines finer and more closely-packed than those in the illustrations of *Ohiolepis* by Gross (1973), Giffin (1980), Friman (1983), Vieth-Schreiner (1983), Pickett et al. (1985), and *?Ohiolepis*-type scales of Liszkowski & Racki (1993). However, one illustration by Wells (1944: fig. 7f) shows small, closely-packed spines, similar to the Broken River specimens. The spines of the Broken River scales overlap (Fig. 8J,M), in contrast to the condition noted by Gross (1973).

The profile of the scales is low and flat, similar to Giffin's (1980) description of the *Ohiolepis* scales from Taemas. Gross (1973) commented that it is hard to differentiate between the crown

and the neck; this is the case with the Broken River scales.

The spines have a round or oval cross-section, without an anterior groove, thus resembling Friman's (1983) species *'Ohiolepis' frohnrathensis*, as discussed above.

Friman (1983) described the ornamentation of *'Ohiolepis' frohnrathensis* as asymmetrical, but according to Gross (1973), the spines on the crown are arranged both concentrically and in diagonal rows, with the earliest formed, smallest spines located in the centre, and later ones added around the edges. In most illustrated specimens in the literature, the spines appear to be approximately symmetrical, subparallel and pointing posteriorly; this is also the case in the Broken River specimens.

The Broken River scales have a subcircular to subrectangular outline, and a flat or slightly concave base. According to Wells (1944), the base of *O. newberryi* may be flat or convex. The base of *'Ohiolepis' frohnrathensis* Friman, 1983 is always anteriorly convex (Friman, 1983), while that of *O.? xitunensis* Wang, 1984 is flat (Wang, 1984).

Cladolepis Wells 1944

TYPE SPECIES

Cladolepis gunnelli Wells, 1944

Cladolepis sp. cf. C. gunnelli
(Fig. 7K-M)

Cladolepis gunnelli Wells 1944: 36,37; pl. 3, figs. 2-7; pl. 8, fig. 4; fig. 6a,b,d.
Cladolepis ornata Wells 1944: fig. 6h.
Cladolepis sp. Wells 1944: fig. 6c,i.
Cladolepis gunnelli Gross 1973: 97-99; pl. 31, figs. 11-17; pl. 32, figs. 1,2.
?Cladolepis gunnelli Gross 1973: pl. 31, figs. 9,10.
Cladolepis? gunnelli Vieth-Schreiner 1983: 151,152; pl. 3, fig. 25.
Cladolepis cf. *gunnelli* Mader 1986: pl. 7, fig. 10.

REMARKS

Cladolepis was erected by Wells (1944) from material from the bone beds of the Cincinnati Arch Region, from horizons subsequently dated by conodonts as *kockelianus* Zone or older (Klapper & Johnson, 1980). The Broken River scales resemble *Cladolepis gunnelli* Wells, 1944 in shape and crown ornamentation, but differ in having a thick, sloping crown rather than the flat thin crown of *C. gunnelli* Wells, 1944. The base is 'convex and acanthodianlike', as Wells (1944) described some of his specimens. The crown ornamentation is also similar to that of *Antarctilamna prisca* Young, 1982, but that form has a completely different base.

MATERIAL

Seven scales - one intact (QMF26100), three broken at posterior, three severely broken or abraded.

LOCALITY AND HORIZON

The scales occurred in three sections (SD190, SD192, SD210) from horizons of the Papilio Formation and the Stanley Limestone Member of the Mytton Formation, dated middle and upper *varcus, hermanni-cristatus* and *asymmetricus* conodont zones.

MEASUREMENTS

The only unbroken scale (QMF26100) measures 1.9mm long, 2.2mm wide and 0.7mm high. All other specimens have the posterior section broken.

DESCRIPTION

The rounded rhombic or subdiamond-shaped crown slopes gently up from the anterior and flattens out towards the posterior (Fig. 7L). The posterior margin is slightly pointed. The crown is covered in curved, concentric low ridges that parallel the lateral margins of the scale, and converge posteriorly. The central anterior part of the crown has short, curved, overlapping ridges; these short central anterior ridges and the anterior part of the longer side ridges are grooved (Fig. 7K). The neck area is shallow to nonexistent, and is not indented. The base is diamond-shaped and gently convex (Fig. 7L,M). The anterior part of the base extends beyond the crown, producing a flat, unornamented rim along the anterolateral margins of the scale (Fig. 7K). The crown overhangs the base posteriorly. Where the base joins onto the neck area, a rim is formed, especially at the posterior (arrow in Fig. 7L).

DISCUSSION

The crown ornamentation resembles that of *Antarctilamna prisca* Young, 1982 with concentric ridges converging posteriorly, and grooves on the anterior part of the ridges. The Broken River scales differ from those of *A. prisca* Young, 1982 by having a large, diamond-shaped, convex base and shallow, broad neck; *A. prisca* Young, 1982 scales have a deeply concave, cup-shaped base and a constricted neck

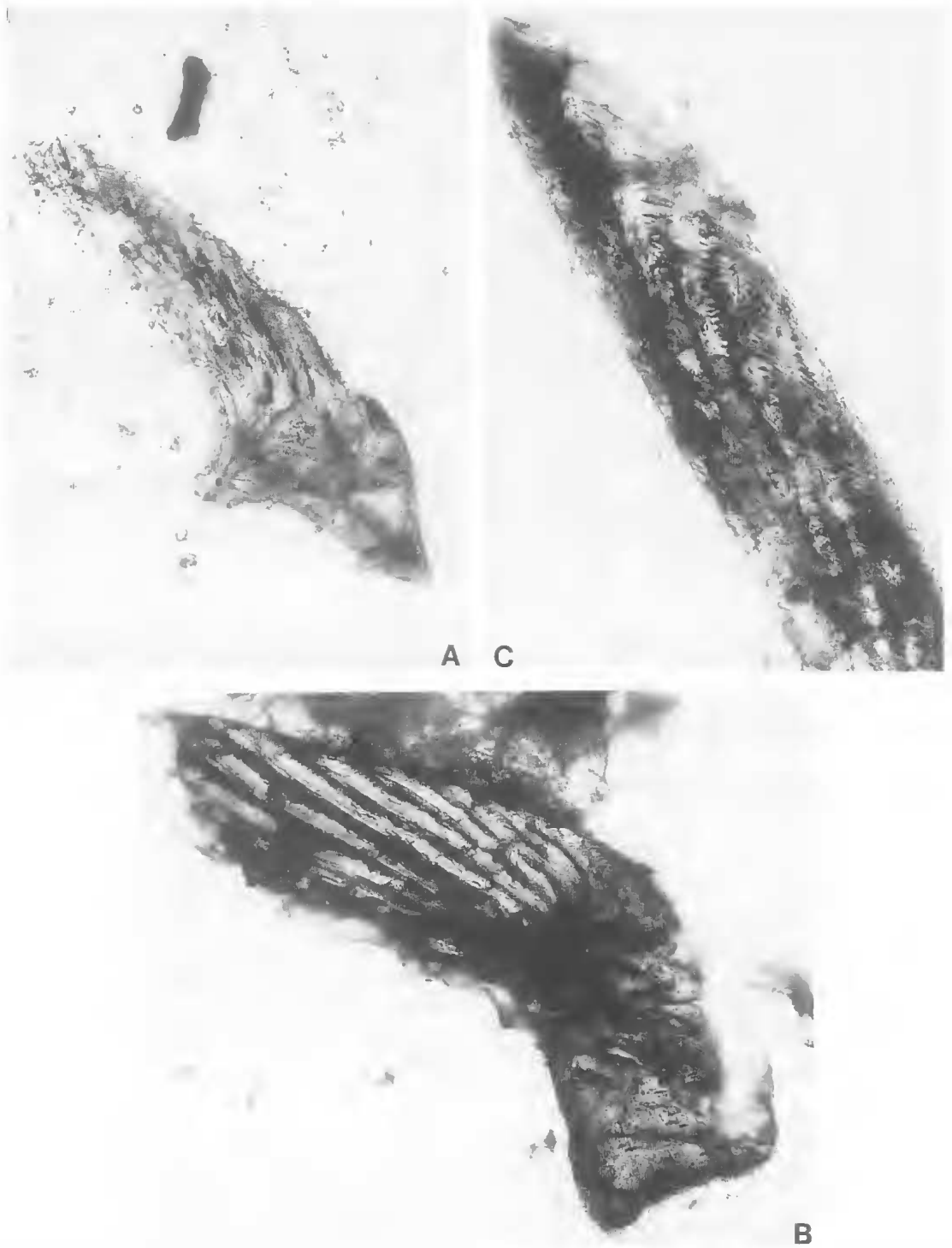

FIG. 12. *Notiolepis dienemos* gen. et sp. nov., SD204/174 upslope. A, longitudinal section QMF31912 of scale, x 45; B, longitudinal section QMF31913 of scale, x 45; C, longitudinal section QMF31914, detail of posterior part of crown, x 90.

(Young, 1982). The Broken River scales also possess several short, flat, curved ridges in the central anterior section of the crown. Such ridges are absent in some scales of *A. prisca* figured by Young (1982: pl. 87, fig. 7; text-figs 2b, 4d); however, one illustrated scale (Young, 1982: pl. 87, fig. 6) shows two short anterior ridges, similar to those present in *Cladolepis*. Enlarged photographs of the holotype of *A. prisca* Young, 1982 show several scales in the dorsal fin area with the short, overlapping, grooved anterior ridges characteristic of *Cladolepis* scales, so this type of scale variation can occur on different parts of the body. Scales referred to *Antarctilamna* sp. by Forey et al. (1992) from the Pragian or early Emsian of Saudi Arabia have superficially similar crown ornamentation to the Broken River specimens. They differ from both the Broken River and *A. prisca* Young, 1982 scales in having finer ornamentation, a larger number of the shorter anterior ridges, and by having the anterior area of shorter, flatter ridges more clearly delineated from the rest of the crown. The scales from both Broken River and Saudi Arabia are a similar size, approximately 2mm; this is slightly larger than the *A. prisca* Young, 1982 scales from Antarctica.

The thick, convex base of the Broken River specimens is similar to that of *Ohiolepis newberryi* Wells, 1944 and *Protacrodus wellsi* Gross, 1973, but the crown ornamentation is different.

Scales from a possible species of *Cladolepis* have been reported from the *gigas* Zone Mostyn Vale Formation near Keepit, NSW (Turner, 1993). Overseas, the genus is known from the early Eifelian Lauch Formation of the Wollenbach member (Vieth-Schreiner, 1983), the Middle Devonian of Indiana (Gross, 1973), the Cincinnati arch region (Wells, 1944), and the middle Givetian to early Eifelian Holy Cross Mountains of Poland (Liszkowski & Racki, 1993). Cladodont teeth are known in Australia, including the Broken River area (Turner, 1982), from Late Devonian and younger horizons.

Chondrichthyan A - fam.,gen. et sp. indet.
(Fig. 10A-C)

MATERIAL
Figured scale QMF 26110 and two other scales.

LOCALITY AND HORIZON
Scale QMF26110 is from section SD15, in the middle *varcus* Conodont Zone Papilio Formation. The other scales occurred in the Papilio Formation of section SD131, dated middle *varcus* Conodont Zone, and the Spanner Limestone of section SD216, dated *hermanni-cristatus* Conodont Zone.

REMARKS
This chondrichthyan scale is not similar to any described form. An unusual feature is a thickened central ridge on the underside of the posterior section of the crown. Examination of more specimens will be required before the scales can be confidently assigned to a genus.

MEASUREMENTS
The scales measure 0.4mm to 0.75mm in length, 0.65mm to 1.2mm in width, and 0.2mm to 0.4mm in height. The length is approximately twice the height, and the width is approximately three times the height.

DESCRIPTION
The crown is wider than long, and slopes up towards the posterior margin. The crown is gently curved at the front, and more pointed at the back. The anterior half of the crown has approximately 12-14 shallow, subparallel ridges, not clearly defined (Fig. 10A). Two or three narrow, low, closely-spaced ridges parallel the posterior margins of the crown. The neck is shallow at the anterior, deeper and clearly indented at the posterior (Fig. 10B). The subtriangular base is flat or gently concave and flared into a thin trim around the edges (Fig. 10B,C), and, like the crown, is wider than it is long.

Chondrichthyan B - fam.,gen. et sp. indet.
(Fig. 10D-G)

MATERIAL
Figured scale QMF26111 and four other scales.

LOCALITY AND HORIZON
The scales occurred in three sections (SD128, SD204 and SD210 - Fig. 2), in horizons of middle *varcus* Conodont Zone age.

REMARKS
The anterior rim and ridges on the crown are similar to those found on scales of the acanthodian *Cheiracanthoides comptus* Wells, 1944 (e.g. Vieth-Schreiner: 1983, pl. 4, fig. 32). How-

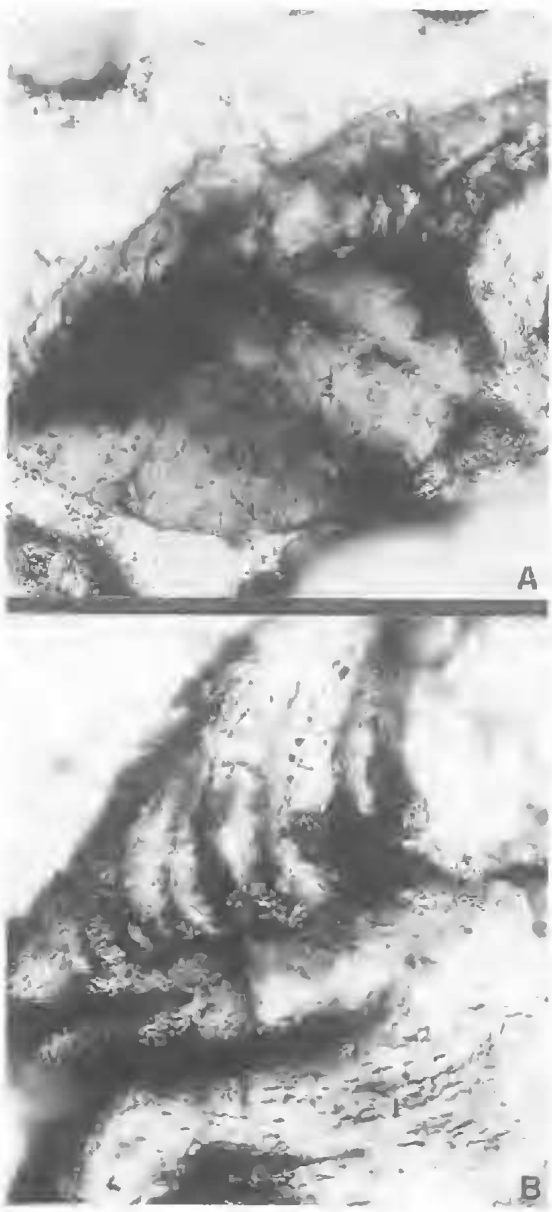

FIG. 13. *Aussilepis lukaso* gen. et sp.nov., SD204/174 upslope. A, longitudinal section QMF26113 of scale showing base and central part of crown, x 60; B, longitudinal section QMF26114, detail of posterior part of scale, showing base and crown, x 80.

ever, these scales from Broken River do not have the shallow neck and deep rounded base typical of acanthodian scales (Turner, 1991). Rather, they have neck canal openings, a relatively high neck, and a flat, diamond-shaped base, distinctive of shark scales (Turner, 1991; Turner & Young, 1987).

MEASUREMENTS

Dimensions of the one intact scale are length 0.6mm, width 0.8mm, and height 0.15mm.

DESCRIPTION

The crown is oval-shaped, thin, and flat (Fig. 10D-G). Seven subparallel ridges extend from the rim at the anterior edge to approximately halfway along the scale; the outer ridges extend into concentric ridges parallel to the posterior margin of the scale (Fig. 10D). The neck is fairly deep, not indented, and has circular canal openings around the posterior edge (Fig. 10G). The base is a narrow diamond shape, elongated across the width of the scale, and is flat (Fig. 10F).

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